Université de Montréal

Variations temporelles des descripteurs des communautés de poissons dans la zone littorale de quatre lacs du Bouclier canadien

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Mémoire présenté à la Faculté des études supérieures
en vue de l'obtention du grade de
Maître ès sciences (M. Sc.)
en sciences biologiques

Décembre 2006

Université de Montréal
Faculté des études supérieures

Ce mémoire intitulé :

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Dans le contexte de crise écologique actuelle, où 35% des espèces nord-américaines de poissons d'eau douce sont menacées, il apparaît essentiel de développer des modèles de qualité des habitats. En établissant des relations entre les attributs de communautés de poissons et certaines caractéristiques importantes de leur environnement, ces modèles peuvent permettre d'établir des cibles claires et efficaces de protection et de conservation des communautés. Le concept même de modèle de qualité des habitats implique qu'à l'intérieur d'une même échelle temporelle (par exemple, au même moment de la journée ou de l'année) les conclusions issues du modèle ne varient pas. Ainsi, un habitat considéré excellent un jour donné doit aussi être considéré excellent le lendemain ou l'année suivante. Alors que plusieurs caractéristiques environnementales des sites sont stables dans le temps, les descripteurs des communautés de poissons peuvent varier à l'intérieur d'une journée, entre les jours et/ou entre les années. Pourtant, les variations temporelles des descripteurs des communautés de poissons, et leurs impacts potentiels sur les modèles, sont souvent ignorés. Les objectifs de ce mémoire sont donc de quantifier la magnitude des variations interjournalières et interannuelles de huit descripteurs des communautés de poissons, pour ensuite tenter de diminuer les variations observées. Deux stratégies ont été étudiées pour réduire la variation interjournalière et interannuelle des descripteurs des communautés de poissons, soit d'attribuer un rang aux sites en fonction de leurs densités en poissons, ou de regrouper en types d'habitat les sites possédant des caractéristiques environnementales similaires.

Quinze sites ont été échantillonnés de façon visuelle dans quatre lacs du Bouclier canadien dans les Laurentides, au Québec. Entre une et trois visites de chacun des sites ont été faites durant les étés 2002 à 2005. Les communautés de poissons ont été décrites, ainsi que plusieurs caractéristiques environnementales de leur milieu. Les descripteurs des communautés de poissons des quatre lacs des Laurentides étudiés ont montré une grande variation entre les jours (entre 2,4 et 209 fois, selon les combinaisons de groupes de poissons, de sites, de lacs et d'années) et entre les années où l'échantillonnage a été mené (de 4 à 950 fois, selon les combinaisons de groupes de poissons, de sites et de lacs). L'attribution de rangs aux sites en fonction de leurs densités en poissons n'a pas diminué cette variation des descripteurs de poissons, ni entre les jours, ni entre les années. Par contre, le groupement des sites en types d'habitats a réduit de façon notable les différences significatives de densités ou de rangs entre les jours et entre les années. Cela suggère que les poissons sont fidèles à certains habitats plutôt qu'à des sites particuliers. Ces informations sont importantes dans la construction de modèles de qualité des habitats valides. Pour que les variations temporelles interjournalières ou interannuelles des descripteurs des communautés de poissons n'influencent pas les relations établies avec les caractéristiques de leur environnement, le regroupement des sites en types d'habitats devrait donc être considéré.

Mots clés : modélisation, variations temporelles, interjournalier, interannuel, habitats, communautés, poissons, zone littorale, lacs, rangs, densités.

SUMMARY

In the current context of ecological crisis, with 35% of North American freshwater fish species threatened, it is essential to develop Fish Habitat Quality Models (FHQM). By establishing relationships between fish community attributes and important environmental conditions, FQHM may allow the designation of clear and efficient protection and conservation targets. The very concept of FQHM implicitly assumes that, within a specified temporal context (e.g. same moment of day or year), conclusions of the models should not vary. Therefore, an habitat designed as excellent one day should also be designed as excellent the following day or year. While many environmental conditions of a site should be temporally stable, fish community descriptors may vary within a day, among days and/or among years. Yet, these temporal variations of fish community descriptors, and their potential impacts on FQHM, are often ignored. Hence, the objectives of this thesis were to quantify the magnitude of among-day and among-year variations of eight fish community descriptors, and then, to explore different strategies to minimize the recorded variations. Two strategies were tested to reduce the among-day and among-year variations of fish community descriptors. The first strategy consisted in ranking the sites according to their fish densities, and the second stategy explored the temporal variations of fish community descriptors when sites that shared similar environmental conditions were grouped in habitat types.

Fifteen sites were visually sampled in four Canadian Shield lakes of the Laurentians, in Québec. One to three surveys of each sampling sites were done during the summers from 2002 to 2005. Fish communities and environmental conditions were described at each site. Fish community descriptors showed great variations among days (from 2.4- to 209-fold, depending on combinations of fish groups, sites, lakes and years) and among years (from 4- to 950-fold, depending on combinations of fish groups, sites and lakes). To rank the sites according to their fish densities did not reduce the among-day or among-year variations of fish community descriptors. However, to group the sites in habitat types considerably minimized the significant differences in densities or ranks among days and among years. This may suggests that fish show fidelity to certain habitat conditions rather than to specific sites. These informations are important in the development of valid FQHM. To prevent erroneous influences of among-day or among-year variations of fish community descriptors on relationships established with environmental conditions, it should be considered to group the sites in habitat types.

Key words : models, temporal variations, among-day, among-year, habitats, communities, fish, lakes, littoral zone, ranks, descriptors, densities.

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FHQM : Fish Habitat Quality Models;

MQHP : Modèles de qualité des habitats de poissons;

GIS : Geographic Information Systems; systèmes d'information géographique;

PCA : Principal Component Analysis; analyse en composantes principales;

ACP : Analyse en composantes principales;

ANOVA : Analysis of Variance; analyse de variance;

d : statistique du test de normalité de Kolmogorov-Smirnov;

p : probabilité;

DF : Diffuse Fidelity; fidélité diffuse;

S.D. : Standard Deviation; écart-type;

SBL : Station de biologie des Laurentides de l'Université de Montréal.

La théorie, c'est quand on sait tout et que
rien ne fonctionne. La pratique, c'est quand
tout fonctionne et que personne ne sait
pourquoi.

Albert Einstein

L'attitude la plus juste chez un honnête
homme consiste à accepter en tout savoir une
part énorme d'inexactitude. L'important n'est
pas de convaincre mais de donner à réfléchir.

Bernard Werber

REMERCIEMENTS

Merci Daniel, pour toutes les heures passées à me faire cheminer à travers le complexe processus d'une maîtrise en écologie. Tous ces moments passés à discuter, à réfléchir, à corriger, à questionner, m'auront permis de développer rigueur, précision et esprit critique qui me seront bien utiles dans ce monde. Merci aussi à Pierre Legendre et André Bouchard pour leur aide précieuse, leur passion et la quantité impressionnante de connaissances qu'ils m'auront permis d'explorer en leur compagnie (j'en suis devenue une scientifique plus productive et plus cultivée, merci! ;-).

Cette aventure n'aurait pas été la même sans la camaraderie et le soutien constants des membres du labo Boisclair. Que de soupirs, de grincements de dents et de fous rires nous aurons partagés!! Merci particulièrement à Judith, Mariane, Marie-Ève B., et Gab pour le support et les encouragements. Merci à Philippe pour le soutien, la stimulation et le bon départ donné à mes études graduées. Vous m'avez tous beaucoup fait grandir.

Merci aux nombreux assistants qui ont participé au travail de terrain: Daniel Lambert, Yann Tissier, Marie-Hélène Léger à l'été 2002; Mathieu Rouleau et Isabelle Barriault à l'été 2003; Mathieu et Nadia Boulé-Lagzhali à l'été 2004; Sylvain Menegat, Gabriel Lanthier, Ariane Cantin et Pascal Lapointe à l'été 2005. Je tiens particulièrement à remercier toute l'équipe de l'été 2005 pour le merveilleux (et tellement intense!) été 2005 passé à la SBL. Ce fut apprécié pour moi autant au niveau personnel que professionnel, et vous pouvez être sûrs que je m'en souviendrai toute ma vie.

Merci à ma garde rapprochée féminine, qui a suivi de près toutes les péripéties et les aventures des mois de cette maîtrise. Ariane, Marie-Pierre, Geneviève B., Geneviève P., Kim, Michelle, Mariane, merci de m'avoir accompagnée autant dans les moments d'excitations intenses que de stress… et j'ai vraiment apprécié les nombreux moments passés en votre compagnie à réfléchir et refaire le monde. Thanks Deo for being there for me with love, support, dreams, many joys and hope... Merci Éli et Steph pour les beaux moments de notre chouette cohabitation et tout le reste, le réconfort, la complicité, les fous rires, les aventures et les rêves partagés. Finalement, merci papa et maman pour votre soutien inébranlable, votre confiance et votre amour…

Sans vous tous, je ne serais pas celle que je suis aujourd'hui et cette maîtrise n'aurait pas été aussi complètement formatrice, aussi profondément inspirante… Merci.

Ce projet n'aurait pas été possible sans la contribution des organismes subventionnaires suivants: le Fonds québécois de recherches sur la nature et les technologies (FQRNT), le Conseil de recherches en sciences naturelles et en génie (CRSNG) et le Comité des études supérieures du Département de Sciences Biologiques de l'Université de Montréal. Merci.

INTRODUCTION

Depuis quelques décennies, les écosystèmes terrestres et aquatiques sont soumis à d'intenses pressions et plusieurs menaces pèsent sur la survie des espèces en Amérique du Nord. Les mammifères et les oiseaux, avec respectivement 13% et 11% d'espèces rares, menacées ou éteintes en Amérique du Nord, ont subit des pertes importantes (Master 1990). Pourtant, c'est dans les milieux aquatiques d'eau douce que l'on a observé le plus de dégâts pour les espèces animales, avec 35% des espèces de poissons d'eau douce nord-américaines qui sont en péril (The Nature Conservancy 2006, IUCN 2006). Ainsi, depuis 100 ans, 27 espèces (dont 3 genres) et 13 sous-espèces de poissons auraient disparu des eaux douces nord-américaines (Miller *et al.* 1989).

Causes du déclin des populations de poissons d'eau douce

Contrairement aux populations marines de poissons, où la pêche industrielle est, et de loin, la principale cause de la diminution de la biomasse de poissons et de l'extinction d'espèces (Pauly *et al.* 2002, Myers et Worm 2003), plusieurs causes expliquent le déclin marqué et l'extinction des populations de poissons d'eau douce. D'abord, l'introduction d'espèces exotiques exerce un stress considérable sur les populations indigènes de poissons en augmentant la compétition et la prédation (Miller *et al.* 1989, Evans *et al.* 1996). La diminution de la diversité génétique causée par les baisses marquées des abondances d'individus est aussi citée comme une menace indirecte pesant sur la survie des espèces et l'intégrité des écosystèmes (Miller *et al.* 1989, Jennings *et al.* 1999). Finalement, la perte et la dégradation des habitats semblent faire consensus parmi les chercheurs comme étant une cause majeure du déclin des populations de poissons d'eau douce (Williams *et al.* 1989, Tilman *et al.* 1994, Richter *et al.* 1997, Reed et Czech 2005). Ainsi, jusqu'à 73% de l'extinction des taxa de poissons (Miller *et al.* 1989) serait due à ce facteur.

Ces perturbations des habitats peuvent prendre plusieurs formes. L'utilisation des terres et la modification des paysages par les humains, soit par la pollution agricole (Karr et Schlosser 1978, Evans *et al.* 1996), la déforestation (Schlosser 1991), et l'érosion (Evans *et al.* 1996) provoquent des perturbations des cycles de l'eau, des sédiments et des nutriments qui modifient profondément la qualité et la disponibilité des habitats pour les poissons (Imhof *et al.* 1996). Aussi, la réduction de la complexité des structures et de l'hétérogénéité du milieu environnant affecte la survie des poissons en éliminant directement certains types d'habitat étant essentiels aux diverses étapes du cycle de vie des poissons (Richmond et Fausch 1995, Christensen *et al.* 1996, Lancaster et Belyea 1997, Le Roy Poff et Huryn 1998, McClanahan et Arthur 2001). L'augmentation de la fragmentation des habitats entraîne également une hausse des risques encourus par les espèces, qui doivent traverser plus de territoires défavorables pour se rendre d'un habitat propice à un autre (Kocik et Ferreri 1998, Palmer *et al.* 2000, Labonne et Gaudin 2006). Finalement, les changements climatiques sont une dernière source de perturbations des habitats pour les poissons. Ils provoquent, entre autres, des hausses des températures des eaux et une diminution de la couverture de glace (Jackson *et al.* 2001, Jones *et al.* 2006).

Étudier les relations entre les poissons et leurs habitats

Dans ce contexte de crise de la biodiversité (Côté et Reynolds 2002) et de sixième grande vague d'extinction massive de l'histoire de la planète (May 1999), il devient essentiel de mener des études afin de comprendre les forces naturelles, anthropiques ou mixtes qui influencent les communautés de poissons. Ainsi, en connaissant les caractéristiques des habitats nécessaires aux poissons pour qu'ils complètent leur cycle de vie, on pourrait assurer plus efficacement la protection et la conservation des populations et des communautés (Souchon et Keith 2001, Olden *et al.* 2002, Quist *et al.* 2004, Torgensen et Close 2004, Rosenfeld et Hatfield 2006). Par leur statut de groupe le plus gros, le plus vieux et le plus diversifié de vertébrés (Master 1990) et leur usage fréquent comme bioindicateurs, les poissons peuvent ainsi servir de taxa modèles pour protéger de larges écosystèmes aquatiques, et contribuer à la conservation de plusieurs organismes moins emblématiques (Angermeier et Schlosser 1995, Minns *et al.* 1996).

Les modèles de qualité des habitats sont des outils qui peuvent permettre de connaître les caractéristiques des habitats essentiels aux poissons et d'établir des cibles de protection et de conservation claires et efficaces. Les modèles de qualité des habitats établissent des relations entre des attributs des populations ou des communautés de poissons et certaines caractéristiques des habitats où elles se trouvent (Boisclair 2001). Bien que la réalité soit plus complexe et moins définie (May 1984), on retrouve généralement dans la littérature deux types de modèles classiques de qualité des habitats: le modèle de contrôle biotique (Lindeman 1942, Southwood 1987) et le modèle de contrôle environnemental (Hutchinson 1953, Whittaker 1956, Bray et Curtis 1957). Le modèle de contrôle biotique attribue à des liens de prédation et de compétition entre les organismes les forces qui structurent les communautés (Wiens 1984, Rossier 1995, Cyterski et Spangler 1996, Gowan et Fausch 2001). Le modèle de contrôle environnemental prétend plutôt que des contraintes environnementales influencent la distribution des individus et la composition des communautés (Dodds et Hisaw 1924, Hall et Werner 1977, Randall *et al.* 1996, Souchon *et al.* 2002, Wei *et al.* 2004). Ainsi, les individus choisiraient un endroit précis selon ses caractéristiques physiques et climatiques, et cela, indépendamment de la densité des populations présentes (May 1984). Hormis ces modèles classiques, on reconnaît aussi l'influence profonde des processus historiques (Karr et Schlosser 1978, Ricklefs 1987, Olden *et al.* 2001, Wiens 2002) et de la structure spatiale (Borcard *et al.* 1992, Borcard et Legendre 1994, Hinch *et al.* 1994, Magalhaes *et al.* 2002) sur les caractéristiques actuelles des communautés. La plupart des études tentent maintenant d'inclure à la fois l'influence de la compétition, de la prédation et des contraintes environnementales, structurelles et/ou historiques dans leurs modèles (Menge et Olson 1990, Eklöv 1997, Fausch 1998, Jackson *et al.* 2001, Taylor *et al.* 2006).

Stabilité temporelle des modèles de qualité des habitats de poissons

De très nombreux modèles de qualité des habitats sont publiés à chaque année, et ce, depuis plusieurs années. Tous ces modèles ne sont pas exempts de problèmes. Souvent, comme le souligne judicieusement Van Horne (2002), ils ne sont pas parfaitement prédictibles, incluent des prémisses biologiquement irréalistes, ne respectent pas les conditions statistiques, omettent les relations causales et/ou ne respectent pas les objectifs de modélisation. Ce mémoire se penchera cependant sur un problème d'un autre genre auquel les chercheurs sont confrontés : celui de la variation temporelle des descripteurs utilisés pour décrire les communautés ou les populations de poissons.

Alors que la plupart des caractéristiques physiques fondamentales des cours d'eau (par exemple, fetch, présence/absence de tributaires, substrat, etc.) sont stables dans le temps, les descripteurs des communautés de poissons (densités, biomasse, diversité des communautés, etc.) sont, eux, sujets à changement. Par exemple, on sait que les poissons se déplacent entre les sites dans les lacs et les rivières, et ce, pour plusieurs raisons. Il y a bien sûr les migrations journalières (Keast *et al.* 1978, Helfman 1981, Luecke et Wurtsbaugh 1993, Appenzeller et Leggett 1995, Gaudreau et Boisclair 2000) et saisonnières (Bryan et Scarnecchia 1992, Chick et McIvor 1994, Gamboa-Pérez et Schmitter-Soto 1999). Certaines espèces migrent aussi pour compléter différentes étapes de leur cycle de vie (Fausch et Young 1995, Schlosser 1995, Schlosser et Angermeier 1995, Albanese *et al.* 2004, Labonne et Gaudin 2006). Les variations temporelles des descripteurs des communautés entre les visites à des sites peuvent aussi être induites par des mécanismes de dynamique des populations. Ainsi, la reproduction ou la compétition (Deacon et Keast 1987, Cyterski et Spangler 1996) et la mortalité (Lyons 1987, Mason et Brandt 1996, Schlosser 1998, Gaudreau et Boisclair 2000) peuvent affecter les abondances de poissons d'une visite à l'autre.

Plusieurs études sont dédiées à décrire spécifiquement ces variations d'abondances ou d'autres descripteurs des communautés dans le temps. Par contre, les objectifs de modélisation des habitats sont autres, soit de comprendre les relations que les poissons entretiennent avec leurs habitats. Dans ce contexte, les variations temporelles des descripteurs des communautés peuvent être une menace à la bonne compréhension des phénomènes en cours. Plusieurs études traitent le problème de la variation des descripteurs en échantillonnant à plusieurs endroits dans l'espace mais pas dans le temps

(Hall et Werner 1977, Poizat et Pont 1996, Weaver *et al.* 1997, Gozlan *et al.* 1998, Perrow *et al.* 1999, Eichbaum Esteves et Lobon-Cervia 2001, Peres-Neto 2004, Turgeon et Rodriguez 2005). Pourtant, à l'intérieur d'une certaine échelle temporelle, l'impact des variations temporelles des descripteurs des communautés sur les conclusions tirées des modèles est incertain. Pour qu'un modèle soit utile et valide, ses conclusions doivent être indépendantes du moment précis où l'échantillonnage a eu lieu; autrement dit, il faut éviter le biais lié au moment où l'échantillonnage a été effectué, à cette photo instantanée de l'écosystème («snapshot», Gowan *et al.* 1994). Bien sûr, on s'attend à ce que des modèles de qualité des habitats dont l'échantillonnage a eu lieu à des moments différents du cycle de vie des espèces, par exemple lorsque les poissons sont en période de reproduction ou en hivernage, ne donnent pas les mêmes conclusions sur les relations entre les poissons et leur habitat. Par contre, des modèles portant sur les mêmes espèces au même moment de leur cycle de vie et dans le même milieu, mais conçus à partir de données échantillonnées à quelques jours d'intervalle par exemple, se doivent d'arriver aux mêmes conclusions pour qu'ils soient utiles et valides. Autrement dit, un habitat désigné comme excellent lors d'une visite doit aussi être désigné comme étant excellent lors de la visite suivante, de la même année ou non. Alors, l'état des connaissances sur les relations entre ces espèces et leurs habitats peut véritablement avancer.

L'importance de la stabilité temporelle des modèles est très grande. Ne pas en tenir compte peut mener à des conclusions erronées sur les caractéristiques des habitats qui sont importantes pour les poissons (Cooper *et al.* 1998) et contribuer à l'instabilité des modèles. Dans un tel contexte, il apparaît primordial d'étudier la variation des descripteurs des communautés dans le temps et d'explorer quelques moyens de minimiser son impact.

Stratégies explorées : rangs et types d'habitat

Dans le cadre de ce mémoire, quatre lacs ont été visités une à trois fois au cours des étés 2002 à 2005 pour décrire les communautés de poissons s'y trouvant et les caractéristiques environnementales de leurs habitats. Cela a permis de répondre à trois objectifs. Le premier objectif était de quantifier l'amplitude des variations interjournalières et interannuelles de descripteurs des communautés de poissons dans les quatre lacs visités. Cela a été fait par plusieurs séries d'analyses de variances à deux critères de classification (ANOVAs) testant les différences de densités de poissons de différents groupes (descripteurs des communautés) entre les sites (premier critère) et entre les jours ou les années (deuxième critère), et ce, indépendamment dans les quatre lacs visités. Les deux autres objectifs visaient à tester deux stratégies afin de minimiser la variation temporelle de densités de poissons observée entre les jours et entre les années dans les lacs.

La première stratégie proposée était d'assigner un rang aux sites selon leur densité absolue de poissons (objectif 2; Lyons 1987, Rahel 1990). En effet, ce n'est pas nécessairement parce que les densités absolues de poissons varient d'une visite à l'autre que leurs relations avec leur habitat sont différentes. Un site ayant les plus fortes densités de poissons lors d'une visite peut toujours avoir les plus fortes densités aux visites suivantes, indépendamment des variations absolues de densités entre les visites. Guay *et al.* (2003) ont ainsi montré que les modèles de qualité des habitats étaient plus efficaces à prédire les rangs des habitats qu'un descripteur spécifique des communautés, dans leur cas la densité de poissons.

La deuxième stratégie était de vérifier les variations interjournalières et interannuelles des descripteurs des communautés de poissons après que les sites aient été groupés en types d'habitat, selon les caractéristiques environnementales qu'ils partagent (objectif 3). En effet, le déplacement des poissons entre les sites n'indique pas nécessairement que leur utilisation des habitats change. Si les poissons se déplacent entre deux sites de macrophytes par exemple, la caractéristique de l'habitat utilisée par les poissons (les macrophytes) est constante. L'étude de Brind'Amour et Boisclair (2006) suggère que les modèles bâtis en regroupant les sites en types d'habitats possédaient un meilleur pouvoir prédictif que lorsque les sites étaient utilisés directement dans les modèles. D'autres études ont aussi regroupé les sites échantillonnés en types d'habitats (Keast *et al.* 1978, Gelwick et Matthews 1990, Brazner et Magnuson 1994, Syms 1995, Randall *et al.* 1996, Vono et Barbosa 2001, Wilson 2001), sans toutefois s'attarder à l'impact de cette démarche sur la variation temporelle des descripteurs des communautés.

Dans le cadre de ce mémoire, l'utilisation des rangs et le groupement des sites en types d'habitats ont donc été testés. Les deux stratégies employées diffèrent selon l'identité de l'élément modifié dans les analyses de variance par rapport aux analyses faites en premier lieu pour tester la variation temporelle des descripteurs des communautés (pour répondre à l'objectif 1). La première stratégie modifie le descripteur des communautés en remplaçant les densités par les rangs, alors que la deuxième stratégie modifie un des deux critères de l'ANOVA, en utilisant les types d'habitats plutôt que les sites. La comparaison des résultats des ANOVAs effectuées a permis d'étudier quelle solution minimise le plus efficacement la variation temporelle des descripteurs des communautés. Cela peut permettre de s'assurer que les relations entre les densités des espèces et leurs habitats ne soient pas des artéfacts issus du fait d'avoir échantillonné différents systèmes à des moments différents (Hinch *et al.* 1991). Des modèles qui reflètent adéquatement les relations réelles existant entre les poissons et leur habitat pourront alors être bâtis afin d'agir efficacement à la protection des espèces et des écosystèmes.

Chapitre 1

Temporal variations of fish community descriptors in the littoral zone of four Canadian Shield Lakes

Résumé

Dans un contexte mondial où les perturbations et les destructions des habitats représentent des menaces sérieuses à la survie des populations et des espèces de poissons, il est important d'étudier les relations existant entre les communautés de poissons et les caractéristiques de leur environnement. De tels modèles de qualité des habitats de poissons (MQHP) sont généralement développés en estimant des descripteurs des communautés de poissons (p.ex. la densité) et des variables environnementales observées dans plusieurs sites à des moments précis. Cependant, des variations temporelles interjournalières ou interannuelles de descripteurs des communautés de poissons à des sites donnés peuvent affecter la validité des MQHP. Les objectifs de cette étude étaient donc de quantifier la magnitude des variations interjournalières et interannuelles de descripteurs des communautés de poissons et de tester différentes stratégies pour réduire les variations temporelles notées. Les deux stratégies étudiées étaient 1) d'allouer un rang aux sites selon leurs densités en poissons et 2) de grouper en types d'habitats les sites qui partagent des caractéristiques environnementales similaires. Quinze sites ont été échantillonnés une à trois fois dans quatre lacs du Bouclier canadien (Québec) au cours de quatre ans. Les caractéristiques environnementales et les communautés de poissons furent décrites à chaque site. Les ANOVAs ont indiqué que la stratégie qui minimisait les variations interjournalières et interannuelles des descripteurs des communautés de poissons était d'utiliser les densités de poissons avec les types d'habitats. Notre étude suggère que l'analyse des densités de poissons avec les types d'habitats peut permettre aux scientifiques de développer des MQHP temporellement plus stables, et conséquemment, plus robustes.

Abstract

In a worldwide context where perturbations and destructions of habitats represent serious threats to the survival of fish species and populations, it is important to study the relationships between fish communities and characteristics of their environment. Such Fish Habitat Quality Models (FHQM) are generally developed by estimating fish community descriptors (e.g. fish density) and environmental conditions observed in numerous sites at specific moments. However, among-day and among-year temporal variations of fish densities at given sites may affect the validity of the FHQM. The objectives of this study were thus to quantify the magnitude of among-day and among-year variations of fish community descriptors and to test different strategies to reduce these recorded temporal variations. The two strategies assessed were 1) to rank the sites according to their fish densities, and 2) to group in habitat types the sites that shared similar environmental conditions. Fifteen sampling sites were surveyed one to three times in four Canadian Shield lakes (Québec) over four years. Environmental conditions and fish communities were described at each site. ANOVAs indicated that fish densities computed over sites that shared similar environmental conditions was the strategy that minimized among-day and among-year variations of fish community descriptors. Our study suggests that the analysis of fish density across habitat types may allow scientists to develop temporally more stable, and consequently, more robust FHQM.

Introduction

North American fish communities have long been recognized to be at risk (Miller et al. 1989). This situation has not improved over the years. For instance, 35% of freshwater fish species are classified as seriously threatened in North America (IUCN 2006, The Nature Conservancy 2006). Habitat degradation is an important cause of the decline of freshwater fish populations (Williams et al 1989, Richter et al 1997, Reed and Czech 2005, Quigley and Harper 2006). Land use practices affect flow regimes, sedimentation patterns, structural complexity, and nutrient release which, in turn, affect habitat quality, quantity, and availability (Schlosser 1991, Brazner and Magnuson 1994, Imholf et al 1996, Christensen et al 1996, Lancaster and Belyea 1997). Introductions of exotic species also affect habitat use by endemic species (Côté and Reynolds 2002).

The conservation of fish species requires the study of habitat characteristics that allow fish to complete their life cycle (Brazner and Beals 1997, Rosenfeld and Hatfield 2006). Fish habitat quality models (FHQM) may be used to assess the effects of environmental conditions on fish communities and to identify habitat characteristics that should be protected for conservation purposes (Pauly et al 2002, Quist et al 2004, Jones et al. 2006). FHQM are relationships between indices of habitat quality at a series of sampling sites and environmental conditions at these sites (Weaver et al. 1997, Vono and Barbosa 2001, Boisclair 2001, Turgeon and Rodriguez 2005). Indices of habitat quality often consist of fish community descriptors (*e.g.* presence/absence, density, and biomass). In these cases, FHQM are developed by estimating fish community descriptors and environmental conditions at specific moments (Lyons 1987, Poizat and Pont 1996, Magalhaes et al. 2002). While many environmental conditions (*e.g.* substrate composition, proximity of tributaries, fetch) observed at one sampling site may not vary significantly among days or even years, most fish community descriptors (densities, biomass, productivity) may be temporally more dynamic (Deacon et Keast 1987, Gowan et al' 1994, Schlosser 1998, Gaudreau and Boisclair 2000, Albanese et al. 2004). This complicates both the development and the application of FHQM that implicitly presume that fish community descriptors taken as habitat quality indices do not vary significantly within a specified temporal context (same time of day, same season, etc). Yet, potential variations of fish community descriptors even within a narrow temporal context are generally ignored.

Recent studies suggest that two strategies may be employed to minimize the temporal variations of fish community descriptors. First, Guay et al. (2003) demonstrated that although FHQM may not always be able to predict specific fish community descriptors (in their study, fish density), they performed better at predicting the rank of habitats (in their study, habitats having the lowest fish densities were ranked 0 and those with the highest fish densities were ranked 1). Second, Brind'Amour and Boisclair (2006) showed that FHQM developed using analytical units (units employed during the statistical analysis performed to develop FHQM) that consist of groupings of sampling sites that share common environmental conditions (same type of habitats) possess a better predictive power than those developed using individual sampling sites.

The objectives of this study were 1) to quantify the magnitude of among-day and among-year variations of fish community descriptors, 2) to estimate the temporal variation of sites ranked according to their fish densities, and 3) to assess the temporal variation of fish community descriptors estimated for sites possessing similar environmental conditions.

Methodology

Lakes and sampling sites

The objectives were achieved by estimating fish community descriptors and environmental conditions at a series of sites located in four lakes of the Laurentian region of Québec (Figure 1) during different days and different years. The study lakes were similar in terms of their surface area (0.155 to 0.260 km^2), mean depth (7.2 to 7.6 m), and total phosphorus concentrations (8.12 to 10.64 µg/L; Table 1). However, these lakes were subjected to different levels of anthropogenic perturbations. The number of cottages or houses *per* watershed ranged from 3 (Lake Violon) to 314 (Lake Sainte-Adèle).

Fifteen sampling sites were selected in each of the study lake. The sampling sites were chosen to represent as accurately as possible the range of environmental conditions found in each lake (from sandy beaches to macrophyte beds and bottoms dominated by boulders). Each sampling site was photographed and georeferenced using a geographic positioning system (GPS 60; Garmin Model, ±5 m).

Sampling of fish communities

Fish communities at each sampling sites were described by performing one (2002 and 2003) to three (2004 and 2005) surveys each year between July 4th and August 10th. Surveys were conducted between 10:00h and 17:00h on days when the cloud cover was <50% and no rain occurred. A sampling site consisted of the area enclosed by a beach seine (height=3.75 m; length=40 m; mesh size of 0.8 cm) deployed from a boat to encompass a water surface extending from shore to the 3 m depth isobaths. The area of the sampling sites averaged 160±26 m^2 depending on their topography. Once the seine was set, an observer snorkelled the complete volume enclosed and classified each fish

Figure 1: Map of the Canadian Shield lakes studied in the Laurentians, Québec, Canada. The four studied lakes are forgrounded and the dark line represent rivière du Nord.

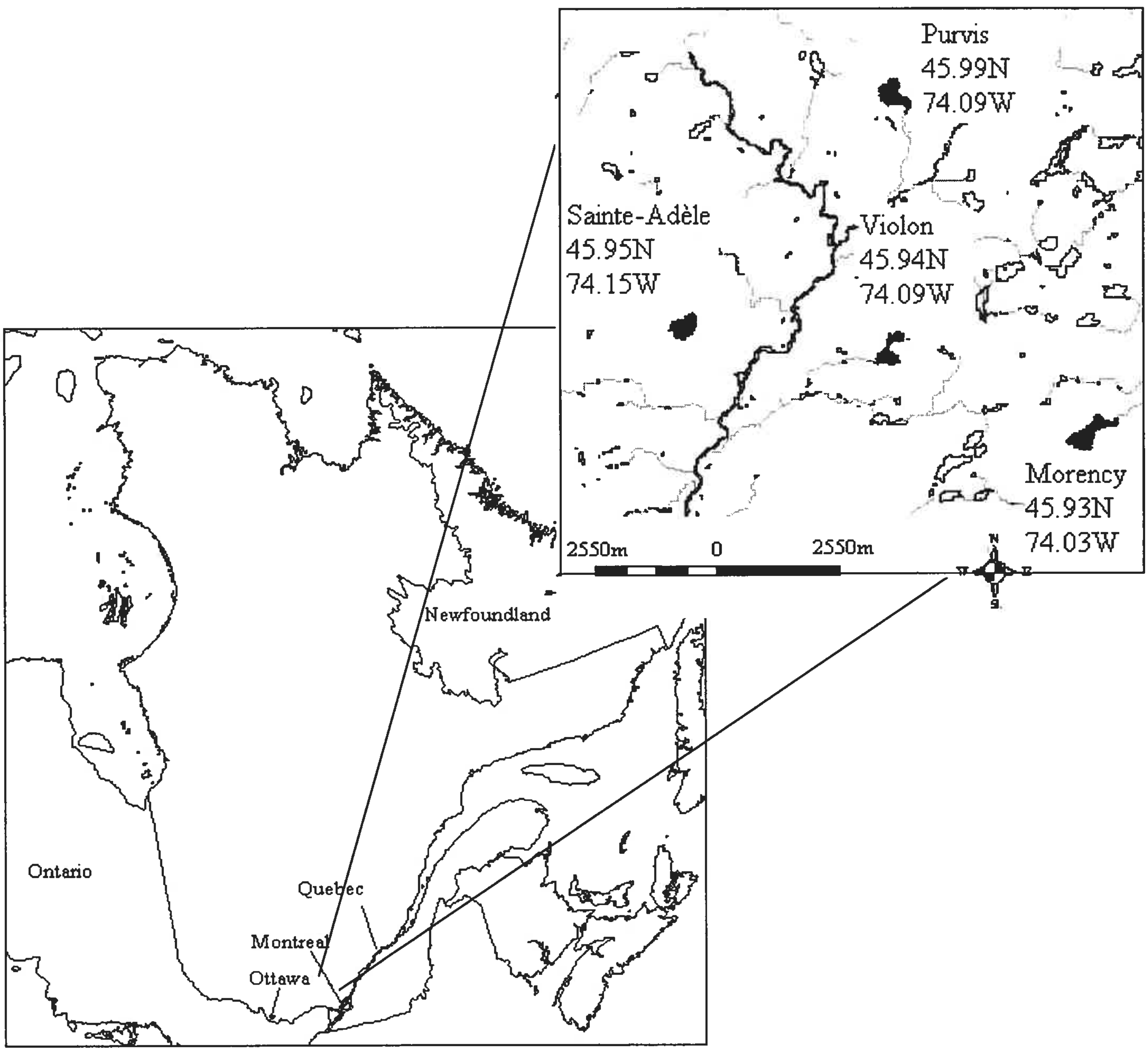


Table 1: Main characteristics of the four Canadian Shield lakes sampled from 2002 to 2005 (Richard Carignan, Université de Montréal, unpublished data). Legend: TP = Total Phosphorus; TN = Total Nitrogen; DOC = Dissolved Organic Carbon; Chla = Chlorophyll a.

Lakes	TP (µg/L)	TN (µg/L)	DOC (mg/L)	Chla (µg/L)	pH	Area (km^2)	Watershed Superficy (km^2)	Altitude (m)	Perimeter (km)	Mean Depth (m)	Number of cottages
Violon	8.12	257.57	2.95	2.03	7.08	0.155	1.748	289	2.471	7.3	3
Purvis	8.71	384.76	2.68	2.35	7.2	0.191	0.6	335	2.444	7.6	27
Morency	8.64	405.07	2.72	2.35	7.38	0.26	2.064	267	3.062	7.5	118
Sainte-Adèle	10.64	488.16	3.08	1.58	8.27	0.166	1.497	281	1.632	7.2	314

by species. This information was noted on white polyvinyl chloride rolls.

Sampling of environmental variables

Environmental conditions at each sampling sites were assessed by estimating eleven variables observed inside the area enclosed by the seine and two variables observed outside each site (riparian use and fetch). Depth at 2 m and 5 m from shore was estimated using a measuring rod (± 2 cm). For the purpose of this experiment, a broad visual survey by a snorkeller of the percent contribution of five size classes of substrate (±10%) was sufficient to describe the main characteristics of the substrate of the sampling sites (Guay *et al* 2000, Table 2). A 900 cm^2 frame was thrown haphazardly ten times inside the area enclosed by the seine. The snorkeller visually evaluated the percent of the surface area inside the frame that was covered by macrophytes and estimated the height of the average macrophyte using a graduated ruler (± 1 cm). The abundance of periphyton was estimated by measuring the thickness of periphyton on ten rocks found within the site with a graduate ruler (± 1 mm; Lambert 2006). Finally, the snorkellers noted the number of trunks (dead trees > 15 cm diameter) inside the sampling site. The shore of each sampling site was defined by four classes of riparian use; open area/grass (class 1), bushes (class 2), thin forest (1-5 trees/100 m^2; class 3), and thick forest (>5 trees/100 m^2; class 4). The length of the fetch (m) at each sampling site was described as the minimum distance between this site and the western shore of the lake because of eastward prevailing winds. The length of the fetch was estimated with a GIS software (ESRI, ArcMap, version 8.3). All environmental variables were estimated during the summer of

Table 2: Description of the environmental variables at each site of the four lakes.

Name	Code	Units
Depth at 2m	DEPTH	m
Silt	SILT	%
Sand	SAND	%
Gravel to Cobble (2mm-250mm)	GRACOB	%
Boulders (250mm-1m)	BOULD	%
Metric boulders (>1m)	METBOUL	%
Height of the average macrophyte	HMACROP	cm
Riparian use	RIPARIUSE	4 classes
Length of the fetch	FETCH	m
Slope of the littoral zone	SLOPE	°
Cover of macrophytes	CMACROP	%
Thickness of periphyton	PERIPH	mm
Density of trunks	TRUNKS	nb/100m²

2005, except for the variables describing macrophytes and periphyton that were estimated during each survey done to quantify fish community descriptors.

Computations

Fish community descriptors

The observations made at each sampling site were used to estimate the densities of four groups of fish; the sunfish (Pumpkinseed sunfish *Lepomis gibbosus* and Rock bass *Ambloplites rupestris*), the minnows (Creek chub *Semotilus atromaculatus*, Bluntnose minnow *Pimephales notatus*, Banded killifish *Fundulus diaphanous*, Fathead minnow *Pimephales promelas*, Golden shiner *Notemigonus crysoleucas*, and Pearl dace *Semotilus margarita*), the piscivores (only Smallmouth bass *Micropterus dolomieui*), and the total fish density (all fish species combined). Fish < 3 cm were not included in the computations because preliminary results suggested that the frequency distributions of the densities of these fish were markedly different from that of the other fish groups. Each sampling site was represented by eight fish community descriptors; the densities of the four fish groups computed for this site and the rank occupied by this site relative to other sites for each of the four fish groups. The ranking employed was adjusted to the purpose of specific statistical analyses (see Statistical analysis).

Environmental variables

The slope of the littoral zone at each sampling site was estimated using the Pythagorean relationship and the depth at 500 cm from shore at this site. The cover of macrophytes and the thickness of periphyton were obtained by averaging the ten observations performed for each of these variables inside the area enclosed by the seine. The density of trunks was estimated by dividing the number of trunks observed within a site by the surface area of this site. Observations performed in the field, obtained using GIS, and computed from field data allowed us to describe each sampling site using thirteen environmental variables (Table 2).

Statistical analyses

Definition of habitat types

The sampling sites of the four lakes were classified in clusters having similar environmental conditions. These clusters are further referred to as habitat types. Habitat types were defined by partitioning the sites according to the thirteen environmental variables estimated for each sampling site (values averaged over all the surveys were used for the height and the cover of macrophytes, and the thickness of periphyton). The variables were standardized to have a mean of zero and a standard deviation of one, because they were not dimensionally homogeneous and in the same physical units (Legendre et Legendre 1998). The partitioning of the sampling sites was performed using a K-Means procedure that allows users to divide a collection of objects into K-groups. The method uses an algorithm that compute cluster centroids and assign each object to the nearest seed to minimize the sum, over all groups, of the squared within-group residuals (i.e. the distance of objects to respective group centroids; Legendre et Legendre 1998). The analysis was done with 1000 permutations to avoid the problem of local minima (Legendre et Legendre 1998). A principal component analysis (PCA) was used to visually represent, in a reduced space, the distance between the sites according to their environmental characteristics. The habitat types defined by the K-Means procedure were then portrayed on the PCA to identify the environmental variables that contributed to the partitioning of the clusters. The PCA was made on the covariance matrix of environmental variables with eigenvectors scaled to a length of one to approximate the Euclidian distances between the sites (Legendre et Legendre 1998). The K-Means analysis and the PCA were done with the Progiciel R (Casgrain and Legendre 2001).

Assessment of temporal variations of fish community descriptors

The temporal variations of fish community descriptors were assessed using eight series of two-way analyses of variance (ANOVA). A series of ANOVA consisted in tests designed to assess the statistical significance of among-site or among-habitat type variations and among-day or among-year variations of fish densities or ranks. Hence, the eight series of ANOVAs differed by the identity of the first (sites or habitat types) or the second (days or years) criteria of the two-way ANOVA and by the identity of the dependent variable (fish densities or ranks). Among-site and among-day variations were tested for each combination of lake, fish group, and year using data collected in 2004 and 2005 (the two years for which the lakes were sampled thrice). This was achieved by assigning each site of a lake with an estimate of fish density (Series 1) or with the rank (Series 2) occupied by this site within 45 sites (3 surveys *per* year x 15 sampling sites; two-way ANOVA without replicates). The sites were ranked 1 (lowest fish density) to 45 (highest fish density) and sites with identical fish densities were attributed a mean rank. Among-habitat type and among-day variations were tested in the same manner with the exception that, as sites were clustered in habitat types, each habitat type was assigned with all fish densities (Series 3) or ranks (Series 4) observed for this habitat type (unbalanced two-way ANOVA with replicates). Among-site and among-year variations were tested for each combination of lake and fish group using data collected in 2002, 2003, 2004, and 2005. During this procedure, each site was assigned with estimates of fish density (Series 5) or rank (Series 6) occupied by this sites within 120 sites (1 survey of 15 sites in 2002 and 2003; 3 surveys of 15 sites in 2004 and 2005). The sites were ranked 1 (lowest fish density) to 120 (highest fish density) and sites with identical fish densities were attributed a mean rank. Fish densities or ranks obtained for the same sites in 2004 and 2005 were employed as replicates (unbalanced two-way ANOVA with replicates). Among-habitat type and among-year variations were tested similarly using either fish densities (Series 7) or ranks (Series 8) as dependent variables (unbalanced two-way ANOVA with replicates). For mathematical reasons presented by Thompson (1991), analyses based on ranks did not allow us to test the interaction between the two criteria (sampling sites or habitat types x days or years).

Fish densities were log-transformed or square-root-transformed when necessary to meet the assumptions of normality required by the ANOVA. The minnows in Lake Morency were the only distribution that could not be normalized. However, their log-density distributions were not too asymmetric (Kolmogorov-Smirnov test of normality; $0.26<d<0.29$; $p<0.01$; Legendre et Legendre 1998). The log-densities of these distributions were used in the analyses because ANOVAs are robust to slight departures from normality (Kutner et al 2005).

The eight series of ANOVA allowed us to identify the approach (analysis of fish density by site; analysis of sites ranked according to their fish density by site; analysis of fish density by habitat type; analysis of sites ranked according to their fish density by habitat type) that minimized the effects of among-day or among-year variations of the fish community descriptors. ANOVAs were done with STATISTICA software (StatSoft Inc., 2001).

Results

Fish community composition

Sunfish were found in the four lakes and represented, on average, 60% of the fish community (range = 21 to 81 %; Table 3). They were particularly dominant in Lakes Violon, Purvis, and Morency where their density was 2- to 5-fold larger than that of minnows and piscivores (Figure 2). Minnows were observed in three lakes (Lakes Violon, Morency, and Sainte-Adèle) and averaged 41% of the fish community (Table 3). Their contribution to the fish community was especially important in Lake Sainte-Adèle where they accounted for as much as 75% of the fish observed. Smallmouth bass were found in three lakes (Lakes Purvis, Morency and Sainte-Adèle) where they represented, on average, 11% of the fish community (range = 4 to 18 %). Other fish species such as Yellow perch (*Perca flavescens*; only in Lake Purvis) and White sucker (*Catostomus commersoni*; only in Lake Violon) contributed to less than 2% of their respective community. Total fish density ranged from 0 to 747 fish/100 m^2 across lakes, sampling sites, days, and years.

Environmental conditions

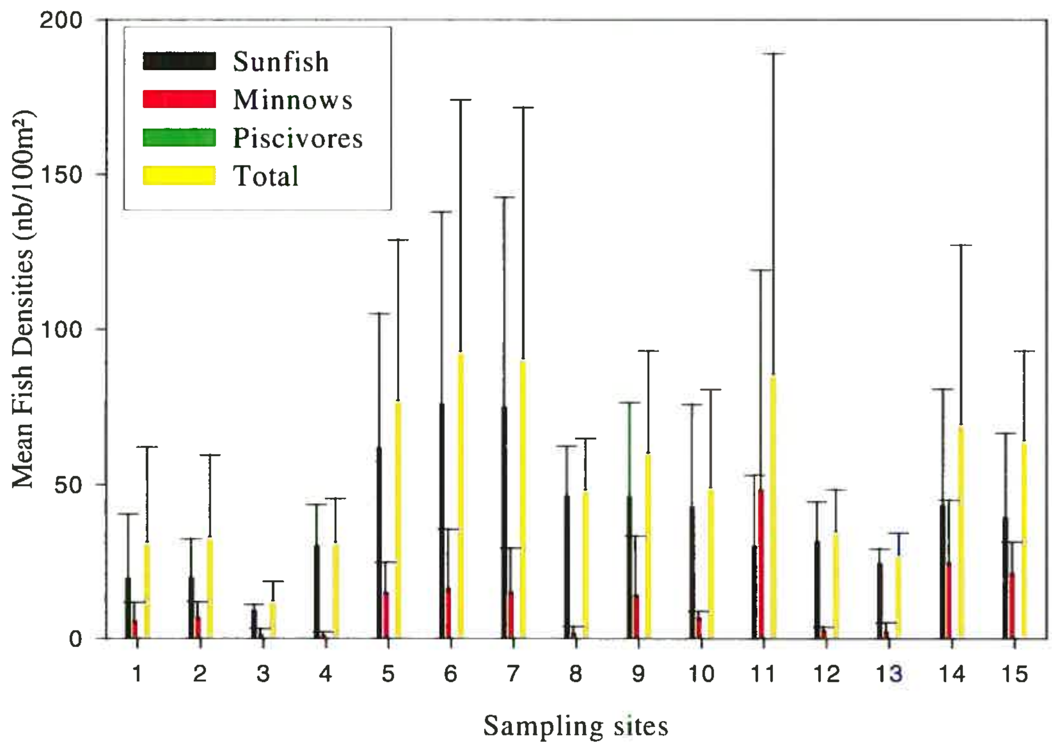
The littoral zones of the four lakes sampled were characterized by the high percent cover of silt (Table 4). On average, silt covered from 52 % (Lake Violon; range = 0 to 90%) to 73 % (Lake Sainte-Adèle; range = 0 to 100%) of the bottom of the sampling sites. The percent contribution of metric boulder was also an important feature of the littoral zone (on average 20-27 % of substrate composition) except for Lake Sainte-Adèle where this substrate covered, on average, only 3 % of the bottom of the sampling sites. Although the percent contribution of sand to the substrate of the littoral zone (4 to 21%)

Table 3. Percent contribution of each group of fish in each lake over the four years. Mean fish densities per lake (# of fish/100m²) are in parentheses.

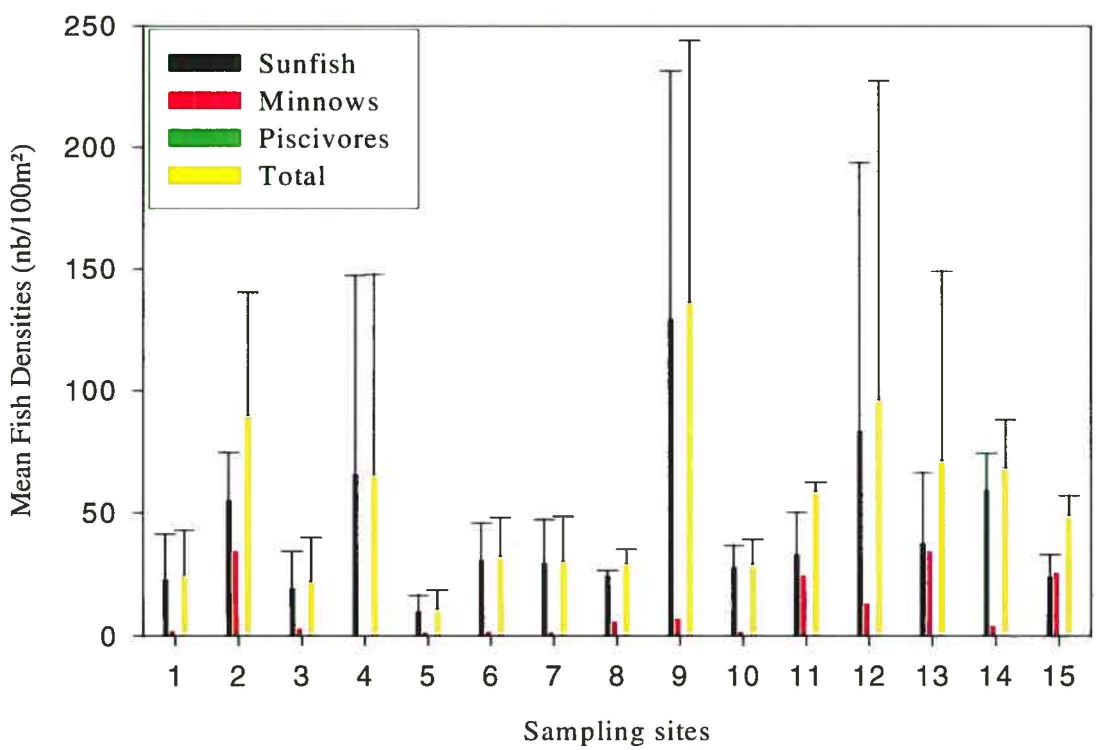
	Lake Violon	Lake Purvis	Lake Morency	Lake Sainte-Adèle
Sunfish	81 (53.3)	80 (23)	57 (75.4)	21 (29.5)
Minnows	17 (11.6)	--	32 (42.1)	75 (103.2)
Piscivores	--	18 (5.2)	11 (15.3)	4 (5)
Others	2 (1.2)	2 (0.4)	0	0
Total	(66.1)	(28.7)	(132.8)	(137.9)

Figure 2: Mean fish densities (# of fish /100m²) at each site for the four groups of fish in the four lakes in 2004 and 2005. The vertical bars represent the standard deviations. a) Lake Violon, b) Lake Purvis, c) Lake Morency, d) Lake Sainte-Adèle.

a)

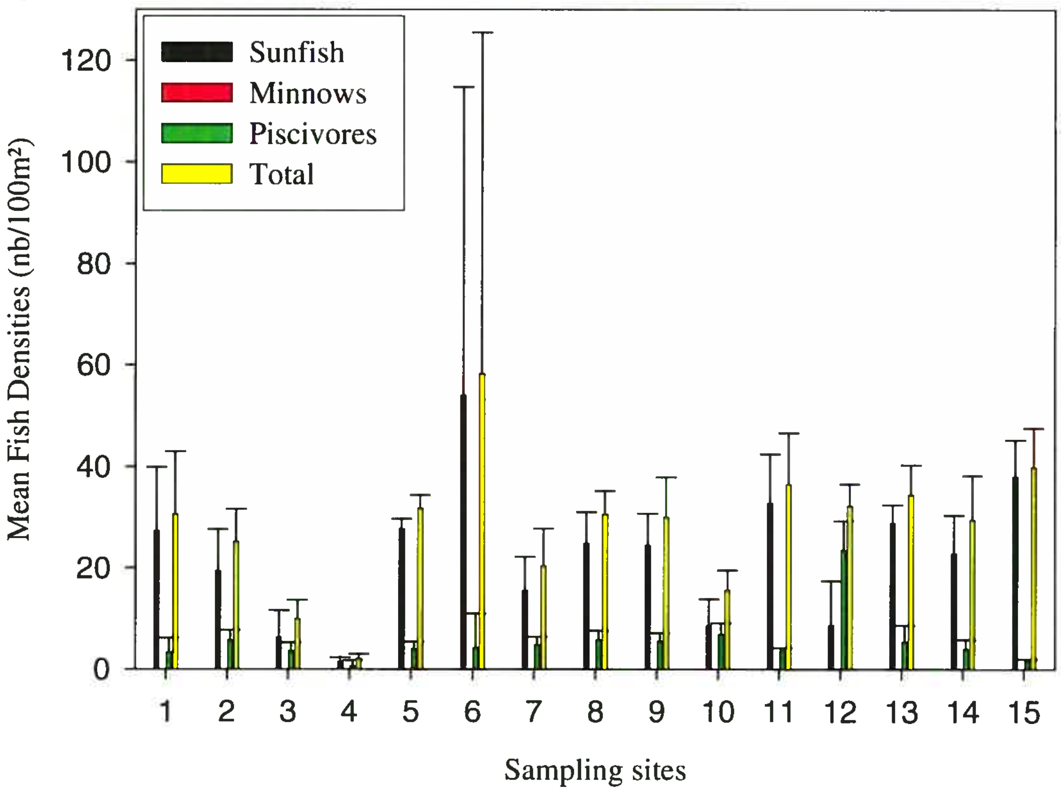


2005



2004

b)


Mean Fish Densities (nb/100m²)
0
20
40
60
80
100
120
Sunfish
Minnows
Piscivores
Total
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3
4
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8
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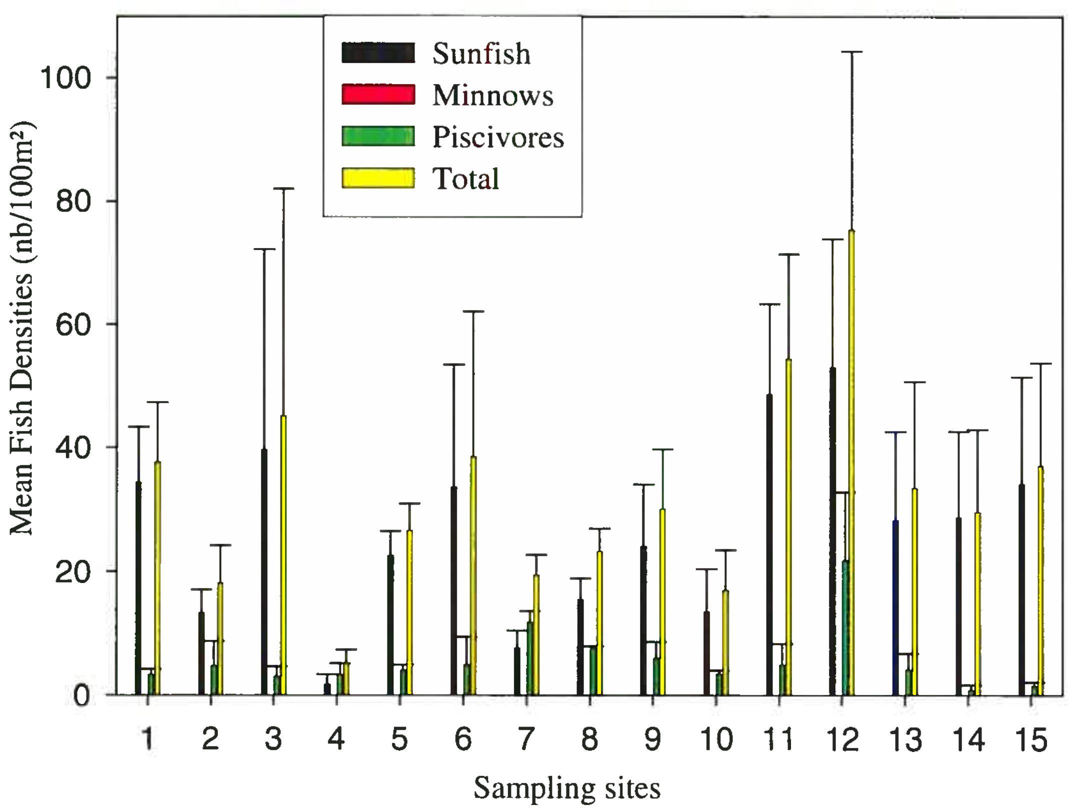
12
13
14
15
Sampling sites

2005


Mean Fish Densities (nb/100m²)
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40
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Sunfish
Minnows
Piscivores
Total
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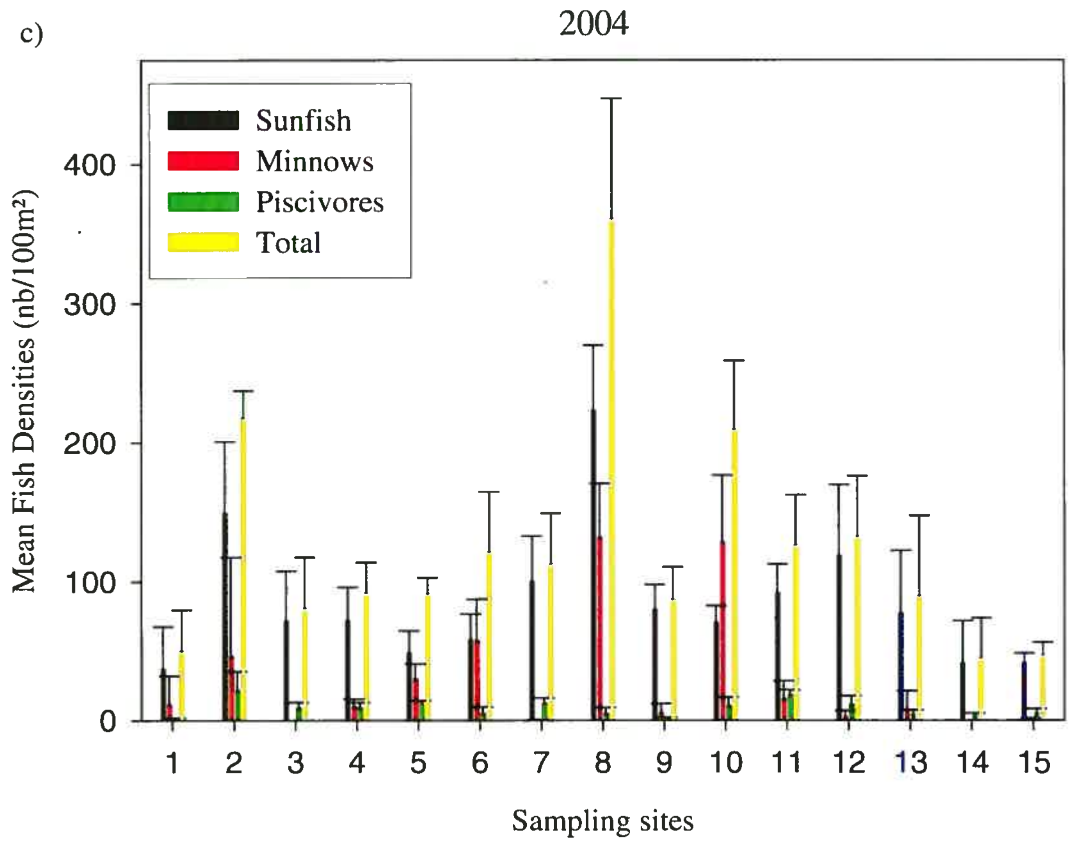
Sampling sites

c)


2004
Sunfish
Minnows
Piscivores
Total
Mean Fish Densities (nb/100m²)
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100
200
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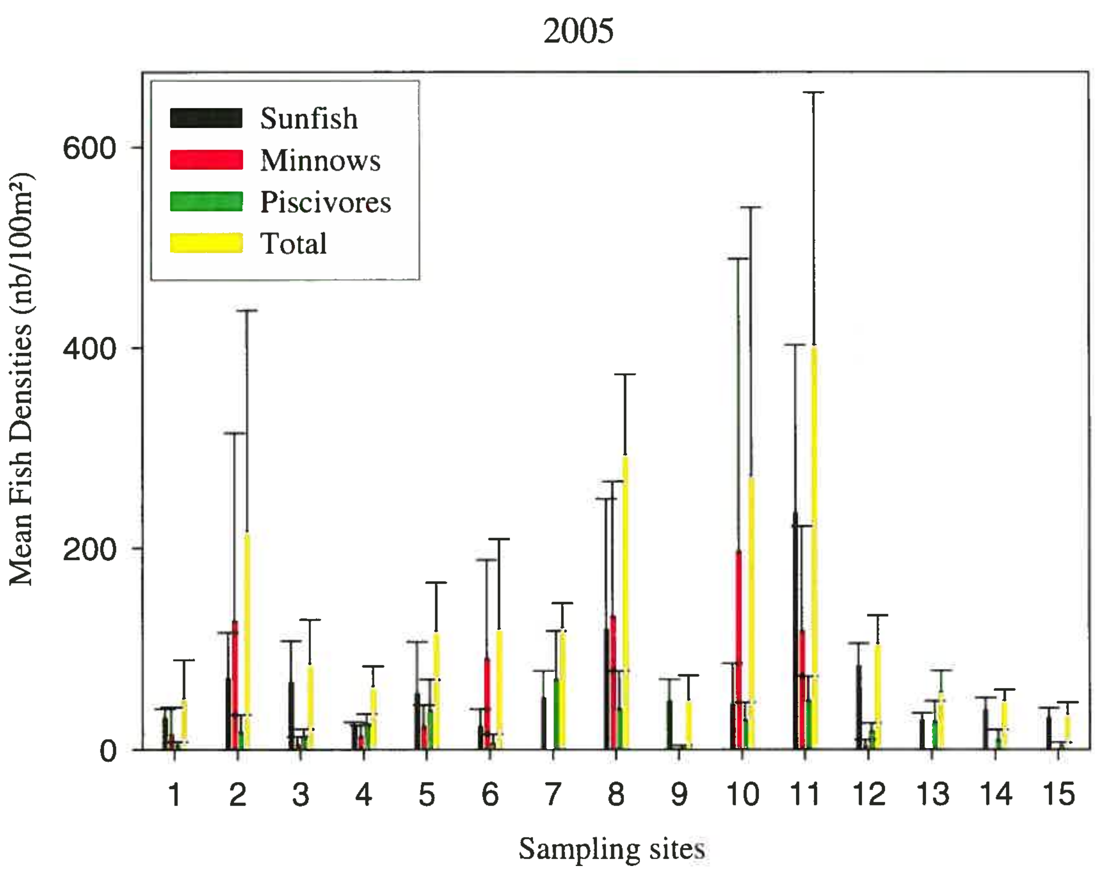
Sampling sites


2005
Sunfish
Minnows
Piscivores
Total
Mean Fish Densities (nb/100m²)
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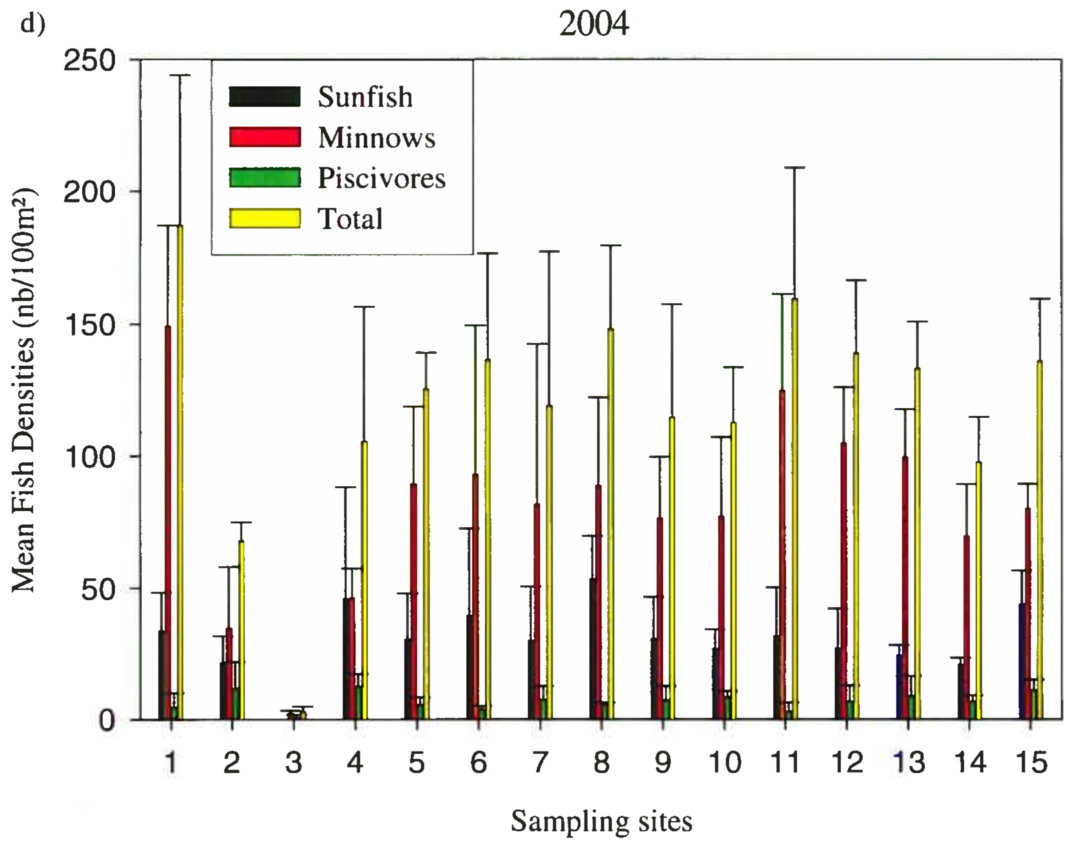
Sampling sites

d)


2004
Sunfish
Minnows
Piscivores
Total
Mean Fish Densities (nb/100m²)
250
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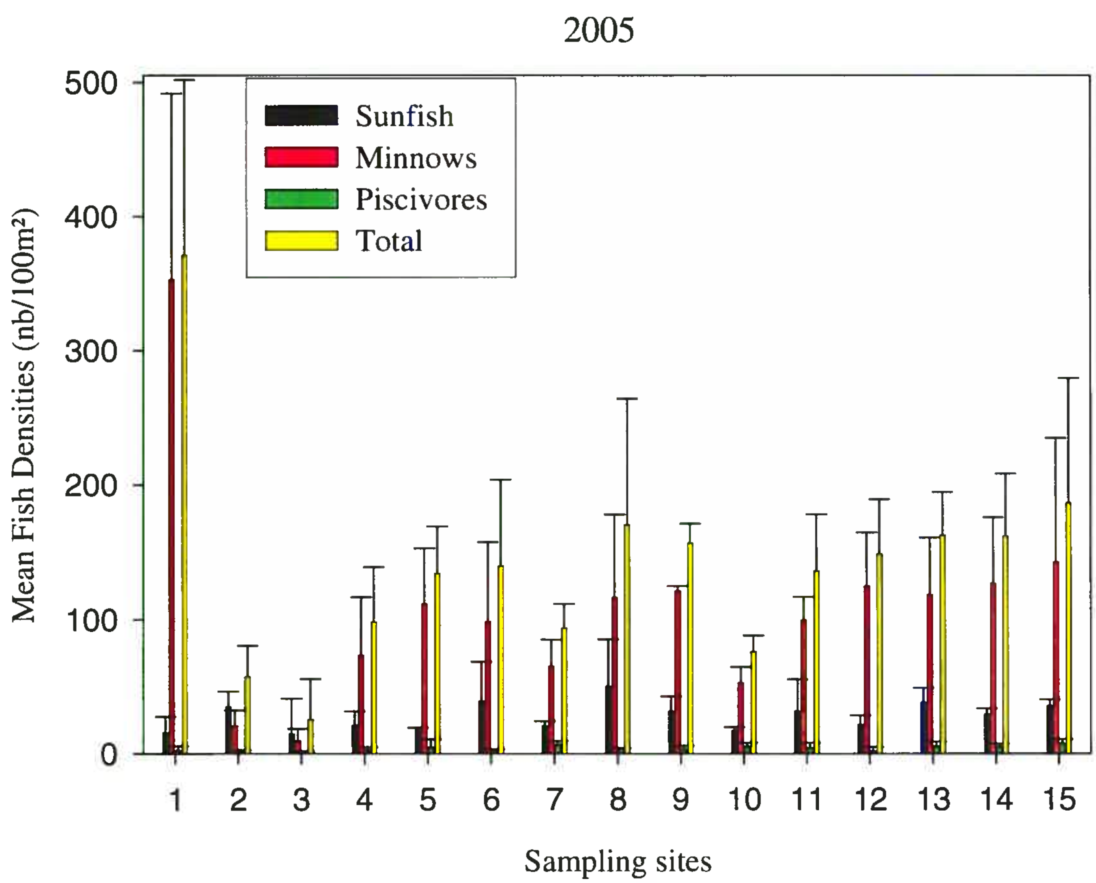
Sampling sites


2005
Sunfish
Minnows
Piscivores
Total
Mean Fish Densities (nb/100m²)
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Sampling sites

Table 4. Means and standard deviations (S.D.) of the environmental variables estimated or computed at each of the fifteen sites of the four lakes sampled. See Table 2 for the codes of the variables.

		Lake Violon	Lake Purvis	Lake Morency	Lake Sainte-Adèle
DEPTH	mean	0.93	0.89	0.70	0.57
	S.D.	0.29	0.63	0.45	0.26
SILT	mean	52.67	55.67	63.33	72.67
	S.D.	28.9	27.96	24.98	32.17
SAND	mean	8	11	4	21.33
	S.D.	22.42	21.89	10.56	34.82
GRACOB	mean	4	3.67	0	0.67
	S.D.	9.1	11.72	0	2.58
BOULD	mean	10.33	9.33	6	2
	S.D.	12.88	13.34	11.83	5.61
METBOUL	mean	25	20.33	26.67	3.33
	S.D.	17.63	18.94	26.09	7.24
HMACROP	mean	19.62	43.25	27.31	55.9
	S.D.	19.94	16.76	22.2	23.93
RIPARIUSE	mean	3.47	3.13	2.8	2.53
	S.D.	1.12	1.36	1.26	1.25
FETCH	mean	178.6	94.67	194.87	76
	S.D.	163.37	138.2	215.6	138.76
SLOPE	mean	11.3	10.76	8.62	6.15
	S.D.	4.67	5.61	5.48	2.98
CMACROP	mean	18.96	17.74	17.44	28.7
	S.D.	10.92	5.07	6.95	10.24
PERIPH	mean	2.16	4.75	4.1	2.28
	S.D.	1.211	2.26	3.2	2.07
TRUNKS	mean	17.54	4.88	2.81	6.65
	S.D.	16.02	5.49	4.78	6.16

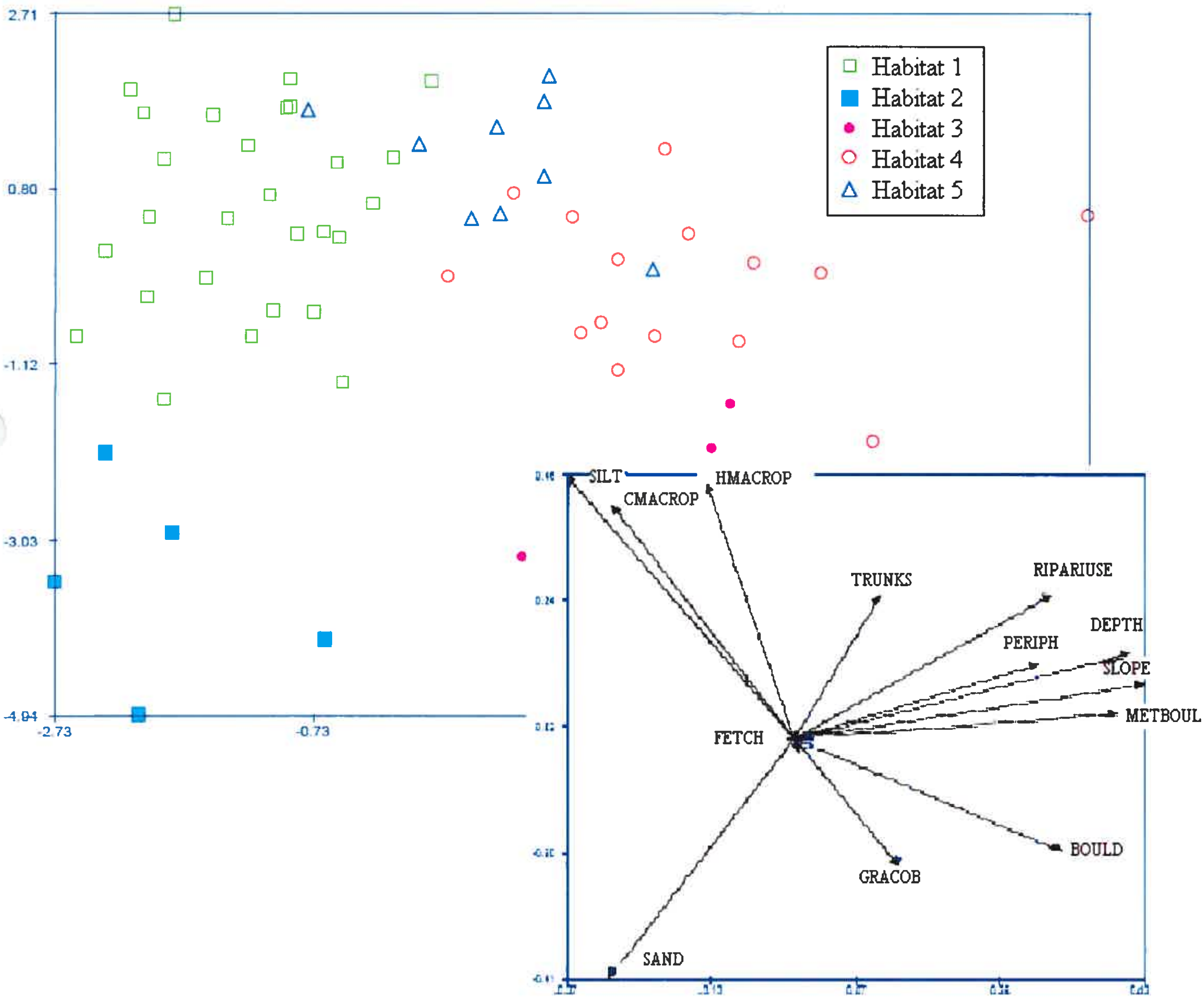
was, on average, 50 % lower than that of silt and 8% lower than that of metric boulder, its coefficients of variation were 2 to 7 times higher than that estimated for the two dominant substrates. The macrophyte cover and the number of trunks were also distinctive among lakes. On average, sites of Lake Violon had a macrophyte cover of 20% (0 to 60%) and 16 trunks/100m^2 (0 to 56 trunks/100m^2) while corresponding values for Lake Sainte-Adèle were respectively 56% (0 to 75%) and 7 trunks/100m^2 (0 to 19 trunks/100m^2). The sites sampled within a lake covered a wide range for the thirteen environmental variables with coefficients of variation from 32 to 280 (Table 4).

Habitat types

Five habitat types were defined by the K-Means analysis (Figure 3). PCA indicated that Habitat 1 consisted of sites that had the highest cover of silt (average= 81%; range= 50 to 100%), the longest macrophytes (average= 24 cm; range=2 to 42 cm), and the highest percent of macrophyte cover (average= 54%; range= 0 to 79%). Habitat 2 comprised sites dominated by sand (average= 72%; range= 40 to 100%). Sites that had a mixture of larger substrate such as gravel and rocks (average of 32%; range=20 to 45%), and boulders (20%) belonged to Habitat 3. Habitat 4 corresponded to the deeper sites (on average, 1.1 m at 2 m from shore, range= 0.3m to 3m) with, on average, 42% of their surface area made up of boulders (range= 0 to 70%) covered by thick periphyton (5.3 mm; from 2 to 8.7 mm). Finally, Habitat 5 comprised sites with a riparian zone consisting in thick forested areas (class 4), and numerous trunks (on average, 27 trunks/100 m^2; range=11 to 56 trunks/100m^2).

The five habitat types were represented in Lake Purvis, while Lake Violon had all habitat types except Habitat 1. Lake Morency had no sites corresponding to Habitat 3 and

Figure 3. Site scores on the first and second axis of PCA (24.4% and 19.8% of explained variance, respectively) for the 60 sites located on the littoral zone of the four lakes. The symbols represent the clusters defined by the K-Means procedure. See Table 2 for the codes of the environmental variables.



5 while all sites sampled in Lake Sainte-Adèle were either sandy beaches (Habitat 2) or macrophyte beds (Habitat 1).

Among-day temporal variations

Among-site and among-day variations of fish densities (Series 1)

The densities of the four fish groups varied among sites and among days in both 2004 and 2005 (Figure 2). Maximum among-site variations of fish densities in Lake Morency ranged from 19- to 950-fold depending on the fish group, the sampling day, and the year. Corresponding variations for Lakes Violon and Sainte-Adèle were 4- to 221-fold and 10- to 164-fold, respectively. Lake Purvis displayed the smallest range of maximum among-site variations of fish densities (31- to 126-fold). Maximum among-day variations of fish densities were quantitatively similar to among-site variations. For instance, in Lake Purvis, maximum among-day variations ranged from 10- to 209-fold depending on the fish groups, sites, and years. Lakes Morency and Violon showed ranges of 21- to 117-fold and 10- to 161-fold while Lake Sainte-Adèle had the smallest range of maximum among-day comparisons with 2.4- to 21-fold. Series 1 consisted in 28 ANOVAs each representing a single combination of lake, fish group, and year. Statistically significant among-site variations of fish densities were detected for 19 of these 28 ANOVAs (Table 5). Series 1 also indicated the presence of 11 statistically significant among-day variations in fish densities. The four fish groups contributed almost equally to the number of statistically significant site effects (four for sunfish, four for minnows, five for piscivores, and six for total fish densities). However, total fish densities tended to be more stable from one day to another (among-day variations

Table 5: Results of the ANOVAs on the among-day differences in densities among sites (series 1). Legend: si=sites, day=days; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001.

Lakes	Community descriptors	2004		2005	
Violon	Sunfish	Fsi=4.60	p=0.0003***	Fsi=1.29	p=0.27
		Fday=38.02	p=0*****	Fday=0.35	p=0.71
	Minnows	Fsi=2.69	p=0.013*	Fsi=2.26	p=0.032*
		Fday=3.94	p=0.03*	Fday=1.00	p=0.38
	Total	Fsi=2.54	p=0.02*	Fsi=1.53	p=0.16
		Fday=25.06	p=0*****	Fday=0.098	p=0.91
Purvis	Sunfish	Fsi=2.64	p=0.01*	Fsi=8.53	p=0*****
		Fday=0.33	p=0.72	Fday=3.91	p=0.032*
	Piscivores	Fsi=6.69	p=0.00001****	Fsi=4.11	p=0.0007***
		Fday=1.91	p=0.17	Fday=1.31	p=0.285
	Total	Fsi=1.49	p=0.18	Fsi=5.69	p=0.00005****
		Fday=0.85	p=0.44	Fday=3.21	p=0.056
Morency	Sunfish	Fsi=4.55	p=0.0003***	Fsi=1.814	p=0.087
		Fday=1.61	p=0.218	Fday=0.311	p=0.735
	Minnows	Fsi=9.12	p=0*****	Fsi=1.619	p=0.135
		Fday=0.581	p=0.566	Fday=5.741	p=0.008**
	Piscivores	Fsi=5.38	p=0.00008****	Fsi=7.35	p=0*****
		Fday=4.136	p=0.027*	Fday=7.79	p=0.002**
	Total	Fsi=7.286	p=0*****	Fsi=4.12	p=0.0007***
		Fday=1.967	p=0.159	Fday=0.399	p=0.675
Sainte-Adèle	Sunfish	Fsi=1.40	p=0.22	Fsi=1.80	p=0.09
		Fday=1.57	p=0.22	Fday=4.36	p=0.02*
	Minnows	Fsi=4.53	p=0.0003***	Fsi=7.25	p=0.00001****
		Fday=4.16	p=0.026*	Fday=1.587	p=0.222
	Piscivores	Fsi=1.75	p=0.101	Fsi=2.58	p=0.016*
		Fday=4.30	p=0.02*	Fday=11.12	p=0.0003***
	Total	Fsi=4.56	p=0.0003***	Fsi=6.08	p=0.00003****
		Fday=1.855	p=0.18	Fday=0.99	p=0.38

detected only once) than other fish groups (three to four statistically significant among-day variations of fish density *per* fish group).

Among-site and among-day variations of the ranks of sites (Series 2)

The number and the structure of the ANOVAs performed under Series 2 were identical to those of Series 1 with the exception that dependent variables were the ranks occupied by the sites in terms of fish densities. Among-site variations of ranks were declared statistically significant for 21 of the 28 ANOVAs (Table 6). The ranks assigned to specific sites (max rank=45 in this analysis) were sometimes very stable (Lake Violon, TFD, 2005; site 11 had ranks 33, 35, 36) and sometimes very variable among-day (Lake Purvis, piscivores, 2005; site 6 had ranks 3, 25, 39.5). Statistically significant among-day variations of ranks were noted for 10 of these ANOVAs. Again, the four fish groups showed a number almost equal of statistically significant site effects (six for sunfish, four for minnows, five for piscivores, and six for total fish densities). Furthermore, almost as in Series 1, no among-day variations were detected for the total fish densities while the other fish groups had two to four statistically significant among-day variations of fish density.

Among-habitat type and among-day variations of fish densities (Series 3)

The 28 ANOVAs performed under Series 3 were similar to those of Series 1, but variations of fish densities were analysed among a maximum of five habitat types (sites belonging to a same habitat type were used as replicates). Habitat type 1 (macrophyte beds) had fish densities (averaged over sampling days) that were 1- to 433-fold larger (average=25-fold) than Habitat type 2 (sandy beaches), depending on the lake and the fish group. Habitat types 4 (deep with metric boulders; average of 11-fold) and 5 (trunks;

Table 6: Results of the ANOVAs on the among-day differences in ranks among sites (series 2). Legend: si=sites, day=days; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001.

Lake	Community descriptors	2004		2005	
Violon	Sunfish	Fsi=3.86	p=0.001**	Fsi=1.33	p=0.25
		Fday=33.895	p=0*****	Fday=0.476	p=0.626
	Minnows	Fsi=2.81	p=0.0098**	Fsi=1.735	p=0.104
		Fday=3.481	p=0.045*	Fday=0.69	p=0.51
	Total	Fsi=2.969	p=0.0069**	Fsi=1.98	p=0.06
		Fday=30.318	p=0*****	Fday=0.084	p=0.92
Purvis	Sunfish	Fsi=3.786	p=0.001**	Fsi=5.03	p=0.00014***
		Fday=0.659	p=0.525	Fday=2.74	p=0.08
	Piscivores	Fsi=2.823	p=0.009**	Fsi=3.636	p=0.002**
		Fday=1.76	p=0.19	Fday=1.869	p=0.173
	Total	Fsi=2.757	p=0.011*	Fsi=3.46	p=0.0025**
		Fday=0.946	p=0.40	Fday=1.972	p=0.158
Morency	Sunfish	Fsi=4.87	p=0.0002***	Fsi=1.568	p=0.151
		Fday=3.26	p=0.053	Fday=0.73	p=0.489
	Minnows	Fsi=7.17	p=0*****	Fsi=3.96	p=0.00095***
		Fday=0.19	p=0.83	Fday=7.267	p=0.003**
	Piscivores	Fsi=6.86	p=0.00001****	Fsi=4.234	p=0.0014**
		Fday=4.63	p=0.018*	Fday=4.234	p=0.0247*
	Total	Fsi=7.97	p=0*****	Fsi=4.83	p=0.0002***
		Fday=2.481	p=0.102	Fday=0.06	p=0.94
Sainte-Adèle	Sunfish	Fsi=1.44	p=0.198	Fsi=2.01	p=0.057
		Fday=1.63	p=0.213	Fday=5.04	p=0.0135*
	Minnows	Fsi=3.88	p=0.001**	Fsi=5.204	p=0.0001***
		Fday=4.559	p=0.019*	Fday=3.07	p=0.062
	Piscivores	Fsi=1.804	p=0.089	Fsi=3.03	p=0.006**
		Fday=4.75	p=0.017*	Fday=12.25	p=0.00015***
	Total	Fsi=2.677	p=0.013*	Fsi=4.26	p=0.0005***
		Fday=2.50	p=0.10	Fday=1.412	p=0.26

average of 8-fold) were intermediate with fish densities 1- to 120-fold larger than that estimated in Habitat type 2 (sandy beaches). However, the fish densities differed on average, 2- to 13-fold among days depending on the lake, the habitat type, the fish groups, and the year. Series 3 underlined the presence of eight statistically significant among-habitat type variations of fish densities while only three among-day variations of fish densities were obtained across the 28 ANOVAs (Table 7). Minnows (three among-habitat type variations), piscivores (three among-habitat type variations), and total fish densities (four among-habitat type variations) displayed similar numbers of statistically significant among-habitat type variations. In contrast, sunfish were the fish group for which we observed the lowest number of habitat type variations (only one). Sunfish (two among-day variations) and total fish densities (one among-day variation) were the only two fish groups that showed statistically significant among-day variations.

Among-habitat types and among-day variations of ranks of sites (Series 4)

ANOVAs of Series 4 presented the same structure than the ANOVAs performed under Series 3, with the exception that the dependent variables were the ranks occupied by the sites in terms of fish densities. Among-habitat type variations of ranks were declared statistically significant for 11 of the 28 ANOVAs performed (Table 8). Sites of the same habitat types sometimes had ranks (max rank=45 in this analysis) very similar (Lake Sainte-Adèle, minnows, 2005; habitat 2 had ranks 1, 2, 3) and sometimes very variable among-day (Lake Purvis, piscivores, 2005; habitat 3 had ranks 2, 29, 37). Statistically significant among-day variations of ranks were noted for 3 of these ANOVAs. The four fish groups contributed almost equally to the number of statistically significant habitat type effects (two for sunfish, one for minnows, four for piscivores, and

Table 7: Results of the ANOVAs on the among-day differences in densities among habitat types (series 3). Legend: h=habitats, day=days; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001. As only two were significant, interactions are not presented in this table.

Lakes	Community descriptors	2004		2005	
Violon	Sunfish	Fh=8.08	p=0.0004***	Fh=1.61	p=0.21
		Fday=19.05	p=0*****	Fday=0.14	p=0.87
	Minnows	Fh=0.94	p=0.43	Fh=1.06	p=0.38
		Fday=1.767	p=0.187	Fday=1.244	p=0.30
	Total	Fh=3.19	p=0.036*	Fh=2.39	p=0.086
		Fday=12.76	p=0.00008****	Fday=0.117	p=0.89
Purvis	Sunfish	Fh=2.26	p=0.09	Fh=23.21	p=0*****
		Fday=0.14	p=0.87	Fday=2.23	p=0.12
	Piscivores	Fh=1.18	p=0.34	Fh=0.98	p=0.43
		Fday=0.081	p=0.92	Fday=0.006	p=0.99
	Total	Fh=1.76	p=0.16	Fh=13.81	p=0*****
		Fday=0.02	p=0.98	Fday=1.10	p=0.34
Morency	Sunfish	Fh=0.062	p=0.94	Fh=0.433	p=0.65
		Fday=0.348	p=0.71	Fday=0.59	p=0.56
	Minnows	Fh=4.07	p=0.025*	Fh=2.60	p=0.088
		Fday=0.008	p=0.99	Fday=1.30	p=0.28
	Piscivores	Fh=2.17	p=0.129	Fh=12.16	p=0.00009****
		Fday=0.38	p=0.689	Fday=2.64	p=0.085
	Total	Fh=0.812	p=0.452	Fh=1.24	p=0.30
		Fday=0.266	p=0.768	Fday=0.116	p=0.89
Sainte-Adèle	Sunfish	Fh=2.278	p=0.139	Fh=1.69	p=0.201
		Fday=1.373	p=0.265	Fday=9.02	p=0.0006***
	Minnows	Fh=4.544	p=0.039*	Fh=11.02	p=0.002**
		Fday=1.706	p=0.195	Fday=0.66	p=0.52
	Piscivores	Fh=7.555	p=0.009**	Fh=6.82	p=0.013*
		Fday=0.58	p=0.56	Fday=2.369	p=0.11
	Total	Fh=7.23	p=0.01*	Fh=6.24	p=0.0168*
		Fday=0.622	p=0.542	Fday=0.158	p=0.85

Table 8: Results of the ANOVAs on the among-day differences in ranks among habitat types (series 4). Legend: h=habitats, day=days; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001.

Lakes	Community descriptors	2004		2005	
Violon	Sunfish	Fhab=6.762	p=0.001**	Fhab=1.92	p=0.146
		Fday=16.76	p=0.00001****	Fday=0.085	p=0.919
	Minnows	Fhab=0.945	p=0.43	Fhab=0.92	p=0.44
		Fday=1.795	p=0.18	Fday=1.515	p=0.235
	Total	Fhab=4.734	p=0.007**	Fhab=3.15	p=0.038*
		Fday=17.09	p=0.00001****	Fday=0.073	p=0.93
Purvis	Sunfish	Fhab=2.23	p=0.089	Fhab=11.75	p=0.00001****
		Fday=0.378	p=0.689	Fday=0.68	p=0.514
	Piscivores	Fhab=2.35	p=0.076	Fhab=1.25	p=0.310
		Fday=0.272	p=0.76	Fday=0.05	p=0.95
	Total	Fhab=2.913	p=0.038*	Fhab=7.905	p=0.00018***
		Fday=0.439	p=0.649	Fday=0.289	p=0.751
Morency	Sunfish	Fhab=0.085	p=0.919	Fhab=0.157	p=0.855
		Fday=0.823	p=0.447	Fday=1.59	p=0.217
	Minnows	Fhab=1.467	p=0.244	Fhab=1.746	p=0.189
		Fday=0.436	p=0.65	Fday=0.27	p=0.764
	Piscivores	Fhab=4.786	p=0.014*	Fhab=7.559	p=0.002**
		Fday=0.44	p=0.645	Fday=1.209	p=0.310
	Total	Fhab=0.754	p=0.478	Fhab=1.176	p=0.32
		Fday=0.418	p=0.66	Fday=0.286	p=0.753
Sainte-Adèle	Sunfish	Fhab=3.788	p=0.059	Fhab=0.235	p=0.63
		Fday=0.56	p=0.575	Fday=6.598	p=0.003**
	Minnows	Fhab=3.27	p=0.078	Fhab=5.273	p=0.027*
		Fday=1.926	p=0.159	Fday=0.359	p=0.70
	Piscivores	Fhab=8.81	p=0.005**	Fhab=8.642	p=0.0055**
		Fday=0.811	p=0.452	Fday=2.784	p=0.074
	Total	Fhab=2.748	p=0.105	Fhab=3.77	p=0.059
		Fday=0.934	p=0.402	Fday=0.122	p=0.885

four for total fish densities). However, sunfish densities tended to be less stable from one day to another (among-day variations detected twice) than other fish groups (only one statistically significant among-day variations for the total fish densities).

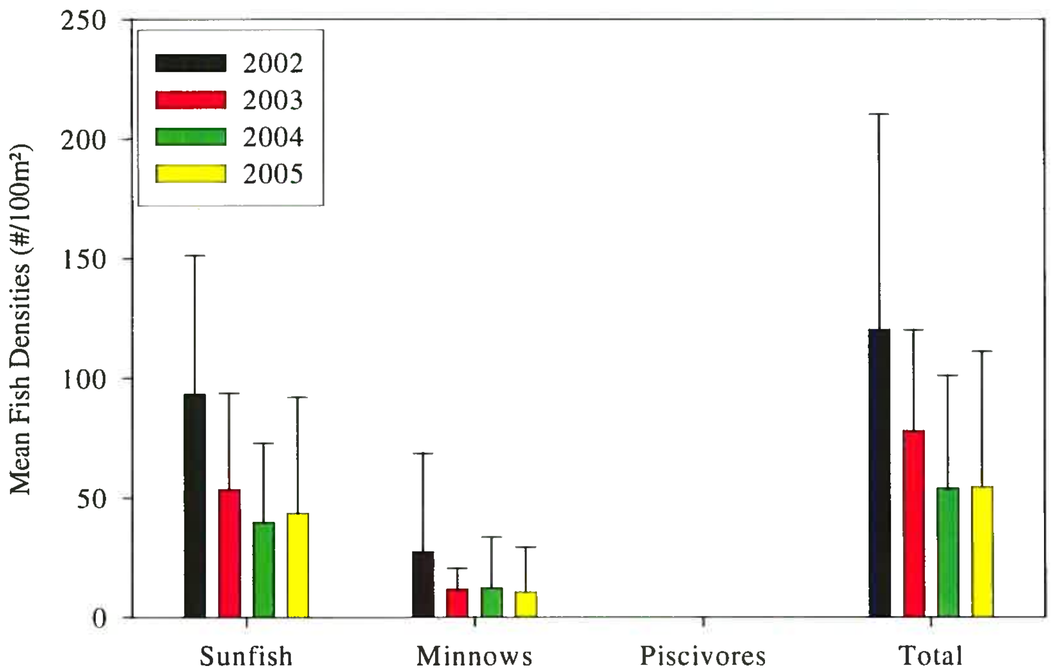
Among-year temporal variations

Among-site and among-year variations of fish densities (series 5)

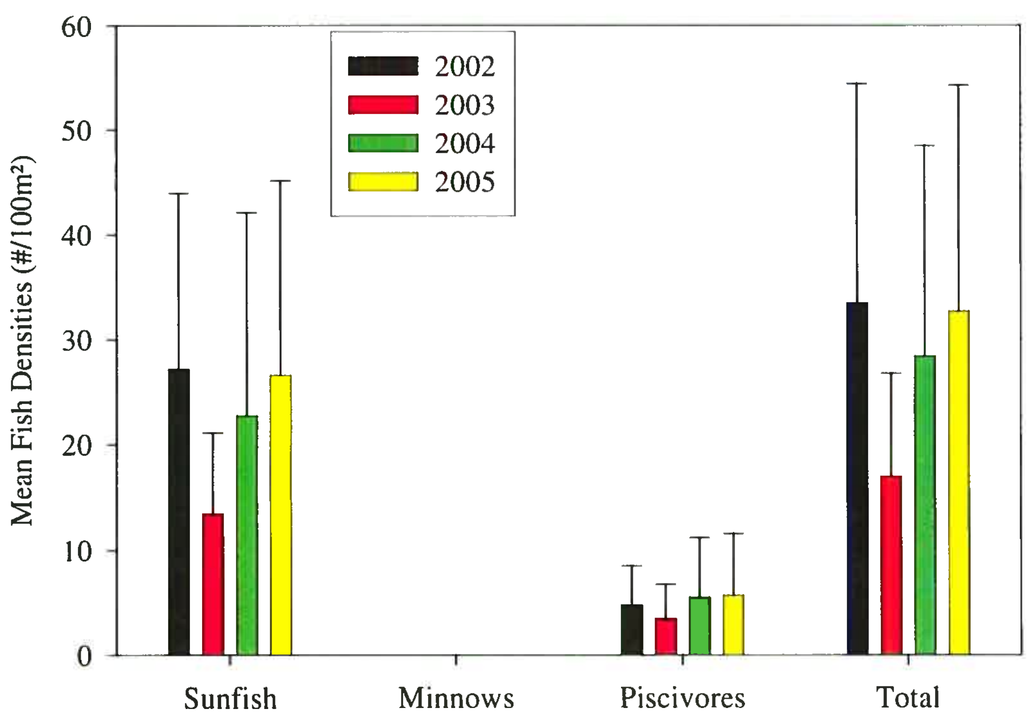
The densities of the four fish groups varied among sites and among years (Figure 4). Lakes Morency (11- to 950-fold) and Violon (4- to 269-fold) displayed the widest range of maximum among-site variations of fish densities, depending on the fish group, the sampling day, and the year. Corresponding variations for Lakes Purvis and Sainte-Adèle were, respectively, 11- to 126-fold and 10- to 194-fold. Maximum among-year variations of fish densities were quantitatively similar to among-site variations. Depending on fish groups, sites and years, the maximum among-year variations ranged from 2.4- to 88-fold in Lake Sainte-Adèle, 10- to 209-fold in Lake Purvis, and 10- to 261-fold in Lake Violon. Lake Morency had the widest range of maximum among-day variations with 14- to 452- fold. Series 5 consisted in 14 ANOVAs each representing a single combination of lake and fish group. Statistically significant among-site variations of fish densities were detected for 13 of these 14 ANOVAs (Table 9). Series 5 also indicated the presence of 10 statistically significant among-year variations in fish densities. Each of the four fish groups presented three to four statistically significant site effects. However, sunfish densities were less stable from one year to another (among-year variations detected in four cases), than other fish groups (two statistically significant among-year variations of fish density *per* fish group).

Figure 4 : Mean fish densities (# of fish /100m²) per site for the four groups of fish in the four lakes from 2002 to 2005. The vertical bars represent the standard deviations. a) Lake Violon, b) Lake Purvis, c) Lake Morency, d) Lake Sainte-Adèle.

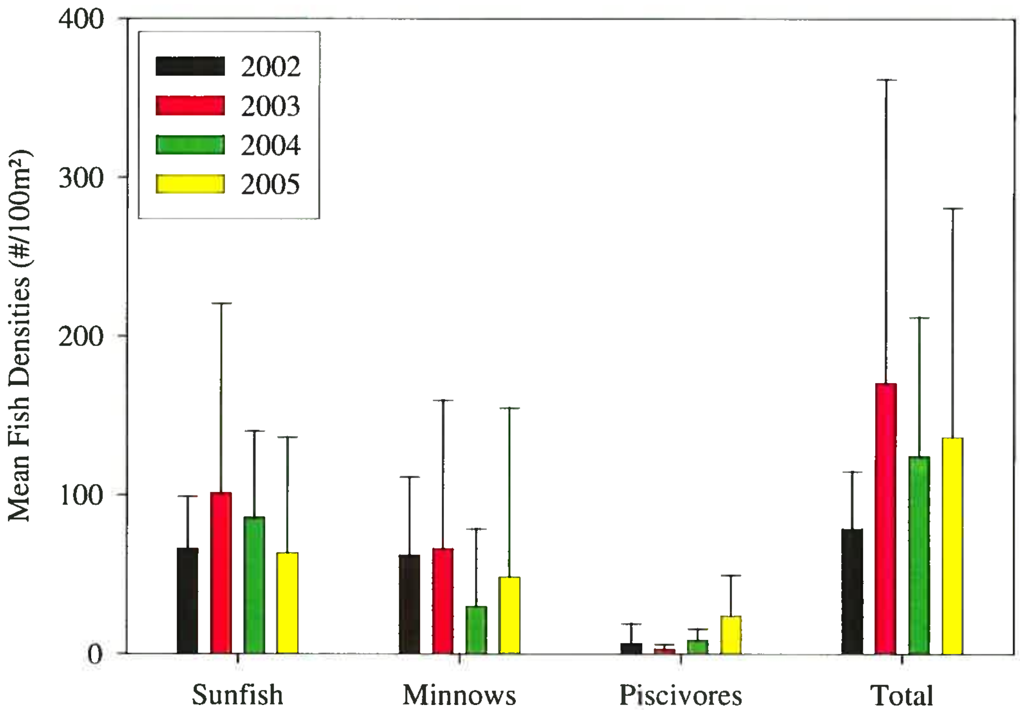
a)



b)



c)


400
300
200
100
0
Mean Fish Densities (#/100m²)
2002
2003
2004
2005
Sunfish
Minnows
Piscivores
Total

d)

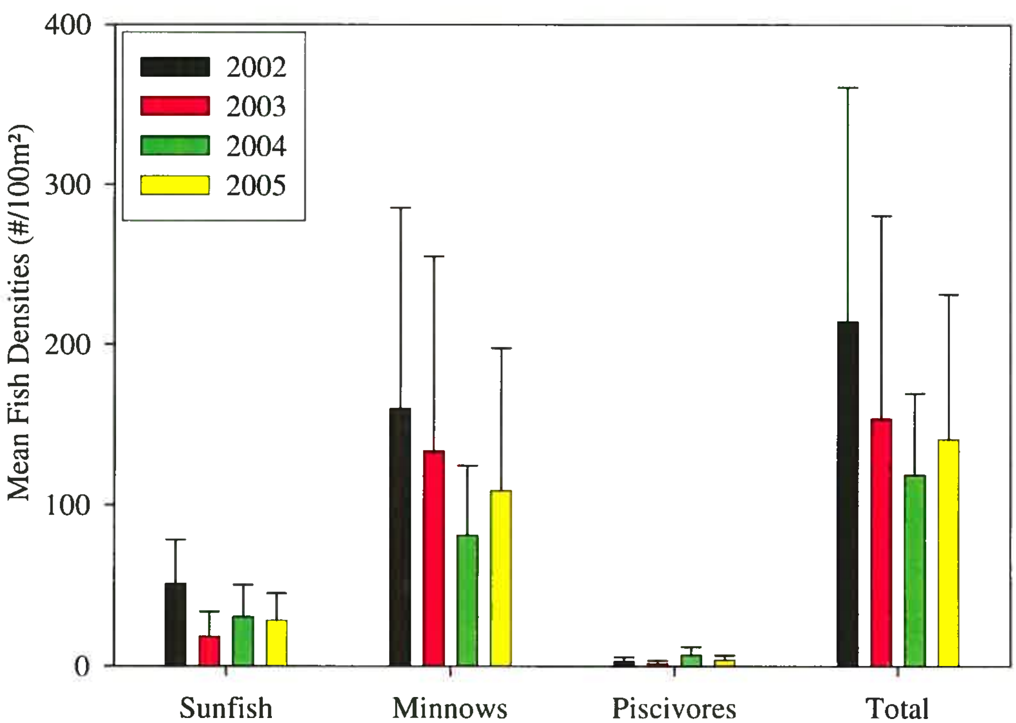

400
300
200
100
0
Mean Fish Densities (#/100m²)
2002
2003
2004
2005
Sunfish
Minnows
Piscivores
Total

Table 9: Results of the ANOVAs on the among-year differences in densities among sites (series 5). Legend: si=sites, y=years; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001.

Lake	Sunfish		Minnows		Piscivores		Total	
Violon	Fsi=2.339	p=0.0077**	Fsi=3.627	p=0.00007****	--	--	Fsi=1.48	p=0.132
	Fy=6.76	p=0.00034***	Fy=3.179	p=0.027*	--	--	Fy=5.37	p=0.0018**
Purvis	Fsi=2.95	p=0.0008***	--	--	Fsi=2.42	p=0*****	Fsi=2.85	p=0.0012**
	Fy=2.857	p=0.041*	--	--	Fy=2.016	p=0.116	Fy=3.2	p=0.026*
Morency	Fsi=4.83	p=0*****	Fsi=6.05	p=0*****	Fsi=8.06	p=0*****	Fsi=6.924	p=0*****
	Fy=5.125	p=0.0025**	Fy=4.662	p=0.004**	Fy= 21.6	p=0*****	Fy=0.653	p=0.583
Sainte-Adèle	Fsi=2.1	p=0.018*	Fsi=7.584	p=0*****	Fsi=2.56	p=0.0036**	Fsi=8.056	p=0*****
	Fy=6.953	p=0.00023***	Fy=2.51	p=0.063	Fy=7.699	p=0.0001***	Fy=1.875	p=0.139

Among-site and among-year variations of the ranks of sites (Series 6)

The number and the structure of the ANOVAs performed under Series 6 were identical to those of Series 5 with the exception that dependent variables were the ranks occupied by the sites in terms of fish densities. A maximum of 120 ranks were attributed to specific sites in this analysis. The ranks of sites were sometimes quite similar (Lake Morency, minnows; site 7 had ranks from 21.5 to 62) relatively to other sites that showed ranks very different (Lake Violon, sunfish; site 4 had ranks from 4 to 116) among years. Among-site and among-year variations of ranks were declared statistically significant in exactly the same cases as for the fish densities of Series 5 (Table 10). Consequently, 13 of the 14 ANOVAs of Series 6 displayed significant effects of sites and 10 ANOVAs presented significant among-year variations of the ranks of the sites.

Among-habitat type and among-year variations of fish densities (Series 7)

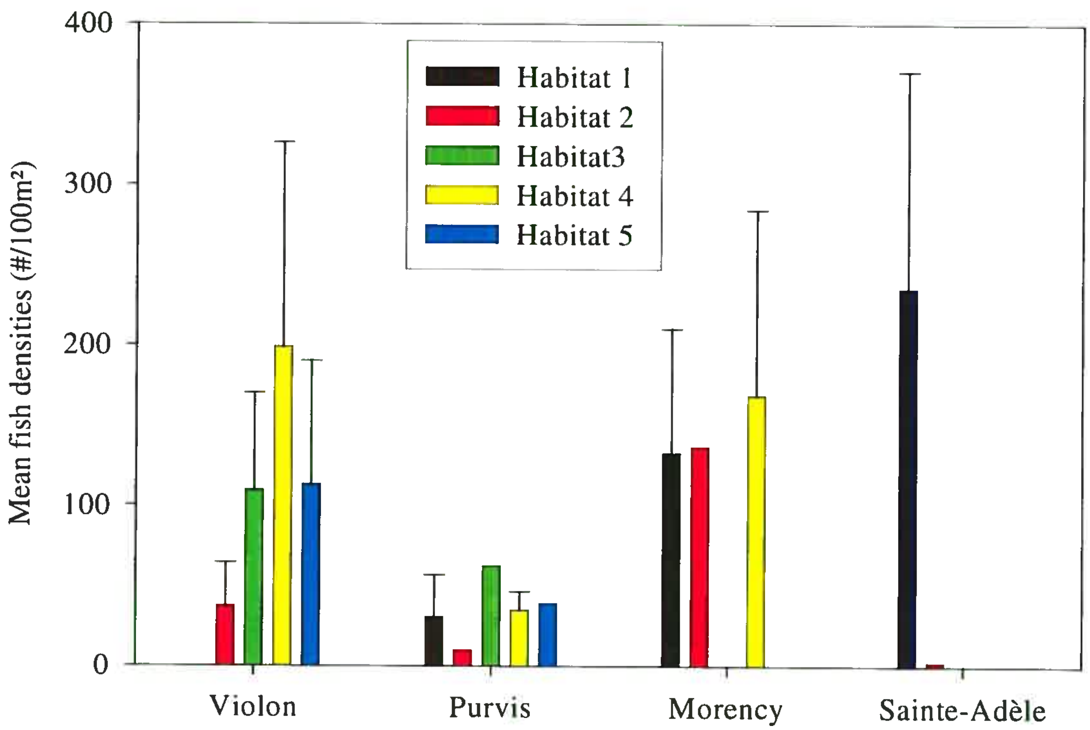
Variations of fish densities were analysed among a maximum of five habitat types for the 14 ANOVAs performed under Series 7. The sites belonging to a same habitat type were used as replicates. Habitat types 1 (macrophyte beds), 4 (deep with metric boulders), and 5 (trunks) had fish densities (averaged over sampling days and years) that differed 1- to 12-fold from Habitat type 2 (sandy beaches), depending on the lake and the fish group (see Figure 5 for total fish density). However, fish densities displayed a maximum variation among years of 2.5- to 408-fold in Lake Morency. Lakes Violon and Sainte-Adèle were intermediate with a range of 2- to 40-fold while Lake Purvis had the smallest among-year variation with a range of 2- to 8-fold. Series 7 underlined the presence of eleven statistically significant among-habitat type variations of fish densities while only four among-year variations of fish densities were obtained across the 14

Table 10: Results of the ANOVAs on the among-year differences in ranks among sites (series 6). Legend: si=sites, y=years; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001.

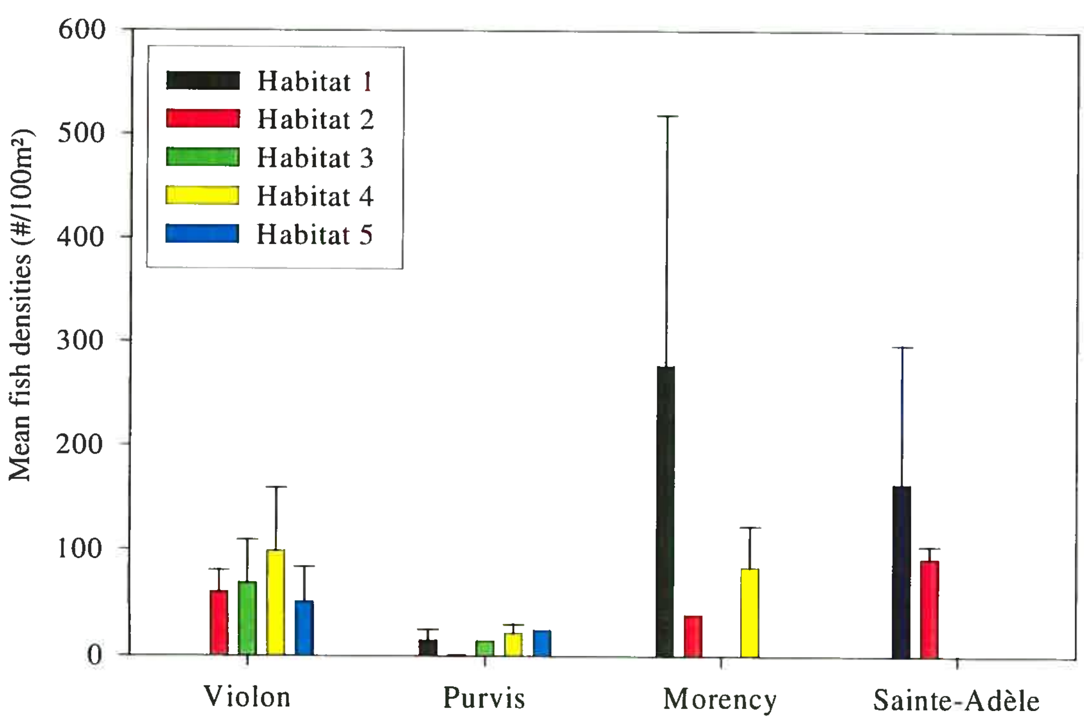
Lake	Sunfish		Minnows		Piscivores		Total	
Violon	Fsi=2.04	p=0.02*	Fsi=3.55	p=0.00009****	--	--	Fsi=1.2	p=0.286
	Fy=7.52	p=0.0001***	Fy=3.44	p=0.0196*	--	--	Fy=5.47	p=0.0016**
Purvis	Fsi=4.813	p=0*****	--	--	Fsi=4.81	p=0*****	Fsi=4.75	p=0*****
	Fy=4.222	p=0.007**	--	--	Fy=1.53	p=0.212	Fy=4.98	p=0.0029**
Morency	Fsi=5.2	p=0*****	Fsi=6.209	p=0*****	Fsi=7.72	p=0*****	Fsi=8.308	p=0*****
	Fy=8.2	p=0.00007****	Fy=4.905	p=0.003**	Fy=22.43	p=0*****	Fy=2.625	p=0.055
Sainte-Adèle	Fsi=2.42	p=0.006**	Fsi=5.98	p=0*****	Fsi=2.58	p=0.003**	Fsi=6.44	p=0*****
	Fy=6.21	p=0.0007***	Fy=1.65	p=0.183	Fy=8.31	p=0.00006****	Fy=1.618	p=019

Figure 5: Mean total fish densities (# of fish/100m²) in the different habitat types of the four lakes for the four years. The vertical bars represent the standard deviations. Analogous results (not shown) were obtained for the other fish groups.
a) 2002, b) 2003, c) 2004, d) 2005.

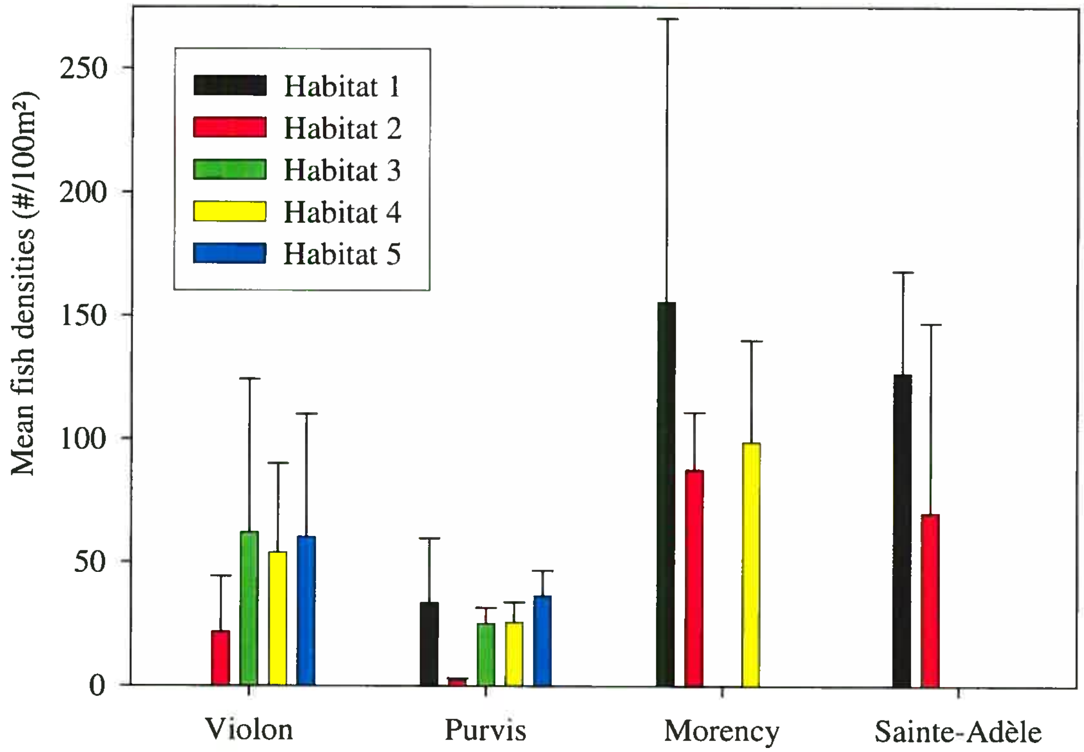
a)



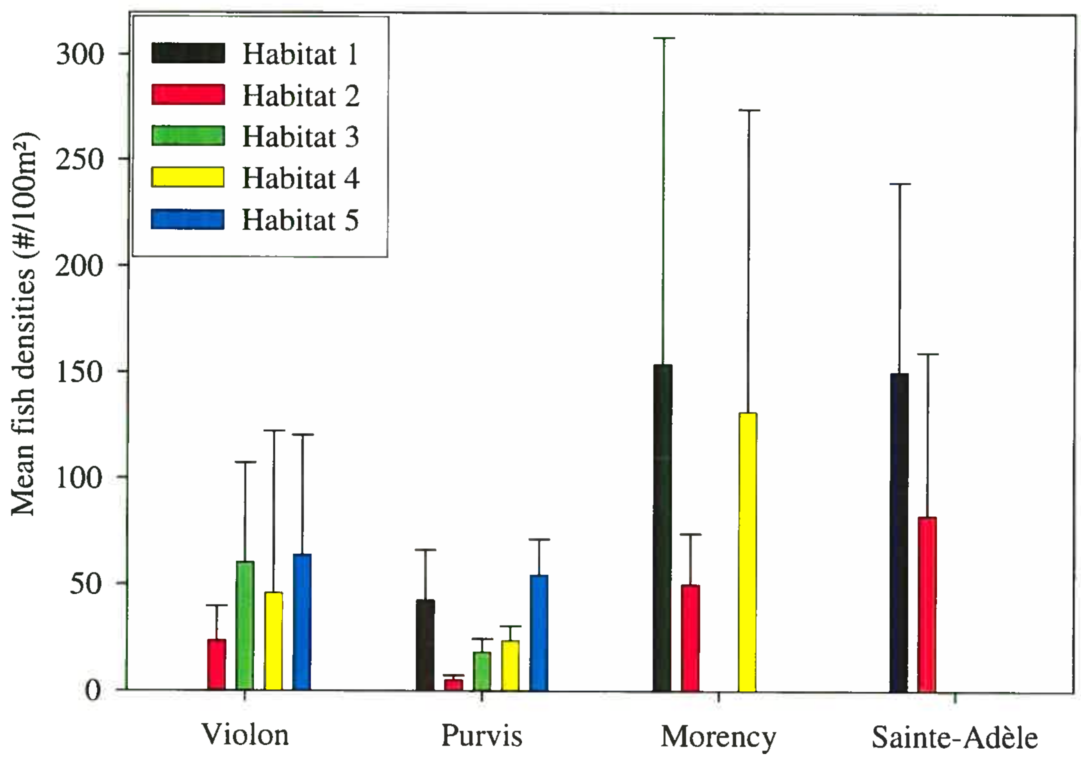
b)



c)


Habitat 1
Habitat 2
Habitat 3
Habitat 4
Habitat 5
Mean fish densities (#/100m²)
0
50
100
150
200
250
Violon
Purvis
Morency
Sainte-Adèle

d)


Habitat 1
Habitat 2
Habitat 3
Habitat 4
Habitat 5
Mean fish densities (#/100m²)
0
50
100
150
200
250
300
Violon
Purvis
Morency
Sainte-Adèle

ANOVAs (Table 11). Three among-habitat type and one among-year variations of density were observed for sunfish, minnows, and piscivores while total fish densities displayed two statistically significant among-habitat type and one among-year variations.

Among-habitat types and among-year variations of ranks of sites (Series 8)

ANOVAs of Series 8 presented the same structure than the ANOVAs performed under Series 7, with the exception that the dependent variables were the ranks occupied by the sites in terms of fish densities. Among-habitat type variations of ranks were declared statistically significant for 11 of the 14 ANOVAs performed (Table 12). Sites of the same habitat types sometimes had ranks (max rank=120 in this analysis) very similar (Lake Purvis, total fish density; habitat 2 had ranks from 5 to 17) and sometimes very variable among-year (Lake Sainte-Adèle, sunfish; habitat 1 had ranks from 3.5 to 116). Statistically significant among-year variations of ranks were noted for 3 of these ANOVAs. The four fish groups contributed to the number of statistically significant habitat type effects in the same way as in Series 7. However, ranks of sites were statistically different among-year in one case for each fish group, except for the minnows.

Table 11: Results of the ANOVAs on the among-year differences in densities among habitat types (series 7). Legend: h=habitats, y=years; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001. As they were not significant, interactions are not presented in this table.

Lake	Sunfish		Minnows		Piscivores		Total	
Violon	Fh=6.144	p=0.00069***	Fh=3.275	p=0.024*	--	--	Fh=2.392	p=0.073
	Fy=5.386	p=0.002**	Fy=1.888	p=0.136	--	--	Fy=5.28	p=0.002**
Purvis	Fh=3.55	p=0.009**	--	--	Fh=5.726	p=0.003***	Fh=3.263	p=0.015*
	Fy=1.826	p=0.147	--	--	Fy=0.481	p=0.696	Fy=1.722	p=0.167
Morency	Fh=0.37	p=0.69	Fh=4.223	p=0.017*	Fh=4.404	p=0.015*	Fh=1.757	p=0.178
	Fy=1.48	p=0.22	Fy=2.782	p=0.045*	Fy=5.02	p=0.003**	Fy=0.668	p=0.574
Sainte-Adèle	Fh=7.348	p=0.008**	Fh=16.208	p=0.0001***	Fh=6.585	p=0.012*	Fh=18.92	p=0.00003****
	Fy=0.649	p=0.585	Fy=1.1	p=0.35	Fy=2.01	p=0.104	Fy=0.699	p=0.555

Table 12: Results of the ANOVAs on the among-year differences in ranks among habitat types (series 8). Legend: h=habitats, y=years; *p<0.05; **p<0.01; ***p<0.001; ****p<0.0001; *****p<0.00001.

Lake	Sunfish		Minnows		Piscivores		Total	
Violon	Fh=5.53	p=0.0015**	Fh=3.138	p=0.029*	--	--	Fh=2.048	p=0.112
	Fy=5.65	p=0.001**	Fy=2.20	p=0.092	--	--	Fy=5.422	p=0.002**
Purvis	Fh=5.819	p=0.0003***	--	--	Fh=5.835	p=0.0003***	Fh=5.32	p=0.0006***
	Fy=2.36	p=0.08	--	--	Fy=0.229	p=0. 876	Fy=2.34	p=0.078
Morency	Fh=0.585	p=0.559	Fh=3.64	p=0.03*	Fh=3.82	p=0.025*	Fh=2.59	p=0.0796
	Fy=2.51	p=0.063	Fy=2.612	p=0.055	Fy=5.49	p=0.0015**	Fy=1.438	p=0.236
Sainte-Adèle	Fh=7.82	p=0.006**	Fh=9.98	p=0.002**	Fh=7.585	p=0.0.0069**	Fh=10.753	p=0.001**
	Fy=0.733	p=0.585	Fy=0.35	p=0.79	Fy=2.301	p=0.081	Fy=0.054	p=0.983

Discussion

Our analyses indicated that the density of four fish groups (sunfish, minnows, piscivores, total fish densities) estimated at specific sites of the littoral zone of four Canadian Shield lakes may vary from 2.4- to 209-fold among days of a summer. The density of fish on the littoral zone of lakes may change from one hour to another because of more or less stochastic movements, between the day and the night because of nyctemeral migrations (Keast *et al.* 1978, Appenzeller et Leggett 1995, Gaudreau et Boisclair 2000), and within the summer because of habitat shifts related to reproduction and feeding (Bryan et Scarnecchia 1992, Fausch et Young 1995, Labonne et Gaudin 2006). Hence, the among-day variations observed during our study were not necessarily surprising. However, these variations pose functional problems to scientists that develop fish habitat quality models (FHQM) and to managers that use them. The very concept of FHQM implicitly assumes that an index of habitat quality such as fish density at a site remains relatively constant at least within a specified temporal context (*e.g.* same time of a day, same period of a season). Violation of this assumption would mean that a site may be defined as an excellent habitat one day and as a poor habitat the next day. This would impede both the development and the application of FHQM. In our study, we attempted to minimize temporal variations of fish density at specific sites by sampling fish during a relatively narrow temporal window (10:00 to 17:00; early-July to mid-August). In addition, sampling was performed under standardized weather conditions (cloud cover <50% and no rain). Despite this strategy, the density of the four fish groups studied varied significantly among days of a given summer in 11 of the 28 analyses we performed to test this variation (combinations of fish groups, lakes, and years). This finding suggests that FHQM that consist of relationships between fish densities and environmental conditions at a series of sites of the littoral zone of lakes may be difficult to develop and eventually to use as predictive tools.

Fish density at a given site may be expected to vary from one year to the next because of fish movements and because of population dynamics driven by yearly variations of reproduction and survival (Deacon et Keast 1987, Cyterski et Spangler 1996, Schlosser 1998). As such, the 4- to 950-fold variations of fish density we observed among years at specific sites were likely to occur. Our results suggested that overall fish densities were effectively higher during some years than others. For instance, average total fish densities in Lake Violon were 2.2-fold higher in 2002 than in 2005. One may expect, however, that a site characterized by environmental conditions that support 'among the highest' fish densities one year may also support 'among the highest' fish densities another year irrespective of absolute densities. Hence, a relative index of habitat quality at a site may minimize the temporal variations of habitat quality indices more efficiently than fish density at this site. This, of course, is contingent to the stability of the environmental conditions employed to describe the habitats. In the lakes we surveyed, the abiotic environmental conditions used to describe the sites displayed such stability. In addition, biotic components such as macrophyte cover did not vary significantly across years ($1.37<F<2.43$; $0.074<p<0.26$), and therefore, the habitat types defined according to the environmental variables sampled were consistent accross years. The index of habitat quality of a site relative to other sites was defined by the rank occupied by this site in terms of fish densities among a series of sites. We therefore anticipated that a site assigned with a low rank (in our study, rank 1 represented the lowest fish density) for one fish group during one year may also have a low rank for that fish group during another year, and this, irrespective of yearly variations of absolute fish densities. Our analyses, which explored the effects of ranking sites on among-day and among-year variations of habitat quality indices, indicated that this operation has no effect on the temporal variation of fish community descriptors. Among-day and among-year variations of ranks assigned to sites (respectively 10/28 and 10/14 of the ANOVAs) were as significant and as numerous as obtained when assigning sites with fish densities (respectively 11/28 and 10/14 of the ANOVAs). The presence of replicates (1-8 ranks assigned to each sampling site) in the ANOVAs performed to test the significance of among-year variations of fish community descriptors further strengthened the interpretation that ranking does not minimize the temporal variation of habitat quality indices assigned to sampling sites. Our study therefore indicated that even when replicates are available, neither fish densities nor ranks may allow the development of temporally robust relationships between fish densities and environmental conditions at a series of sites. Furthermore, t

Our analyses showed that using fish densities of sites that share common environmental conditions as replicates of habitat quality indices for the habitat type that are defined by these sites may considerably decrease the frequency of among-day (only 3 statistically significant variations among the 28 ANOVAs performed) and among-year (only 4 statistically significant variations among the 14 ANOVAs performed) variation of fish community descriptors. This suggests that the analysis of fish densities found in different types of habitats may allow the development of FHQM that minimize the problems raised by among-day and among-year variations of the density of fish groups. Our study is therefore consistent with the findings of Brind'Amour and Boisclair (2006) who proposed that the grouping of sites possessing similar environmental conditions may improve the quality of FHQM. However, our work complements that of Brind'Amour and Boisclair (2006) by showing that the advantages provided by the use of habitat types are not only found in their study lake but also in four different lakes possessing different fish community structures. In addition, although this remains to be thoroughly tested, our analyses point to the possibility that grouping sites in habitat types may not only be useful to develop FHQM that are more powerful during one particular summer, but also among summers of different years.

Site fidelity is the process by which an individual fish repeatedly uses a given location for a specific purpose such as reproduction or feeding (Switzer 1993, Cunjak et al 2005). Site fidelity (and the territoriality that sometimes occurs with it) is a behaviour that facilitates both the development and the use of FHQM because it decreases the temporal variation of the association between fish and environmental conditions. This may explain that most FHQM focused on fish that are known, or expected, to display site fidelity or territoriality (Heggenes and Salveit 1990, Dunham 2002, Waters and Noble 2004). Although some of the nine fish species we observed are known to guard their nests, our observations were performed outside the part of the reproductive period when these behaviours are expected to occur (e.g. sunfish; McCairns and Fox 2004). Our sampling strategy did not allow us to determine the use of sites or habitat types by individual fish. As such, the interpretation that may be developed based on our data may be more 'diffuse' than what could be done using site or habitat utilization by individual fish. However, our sampling did allow us to assess the extent to which specific fish groups consistently had higher or lower densities in particular sites or habitat types. This is further referred to as diffuse fidelity (DF). The small number of among-day and among-year variations of fish densities analysed using the habitat types (Tables 7 and 11) instead of the sites as factors (Tables 5 and 9) is taken as an indication that DF for habitat types is stronger than DF for sites. It therefore suggests that fish move among sites, but generally among sites that share similar environmental conditions. Notably, this applies to among-day and among-year variations and appears to be true for all fish groups analyzed. All fish groups also tended to have significantly higher densities in certain types of habitats than others but this varied among fish groups. For instance, Habitat type 1 (macrophyte beds) had higher densities of minnows in Lake Morency and Sainte-Adèle, while sunfish showed maximum densities in Habitat types 3 (boulders) and 5 (trunks) in Lake Violon and piscivores in Habitat type 4 (deep sites with metric boulders) in Lake Purvis.

Fish distribution in the littoral zone of lakes may be the result of a combination of more or less stochastic movements, well defined migrations, and population dynamics. However, our results suggested that, as these processes take place, fish groups redistribute themselves from sites having certain environmental conditions to other sites having similar environmental conditions thereby displaying a DF for particular habitat types more than for particular sites. The present study indicated that using average fish densities by habitat types may allow scientists to develop FHQM that are robust to among-day and among-year variations of fish density and this, even for fish species that do not display site fidelity.

CONCLUSIONS GÉNÉRALES

Dans un contexte mondial où plusieurs menaces pèsent sur la survie des populations et des communautés de poissons, l'importance de comprendre les relations entre les poissons et leurs habitats est grande. Les modèles de qualité des habitats sont, à ce titre, des outils puissants qui peuvent permettre de cibler les moyens à prendre pour protéger les espèces et l'intégrité des écosystèmes dont elles font partie. Cependant, plusieurs pièges attendent les chercheurs dans la conception de modèles fiables et valides. Le problème de leur stabilité temporelle en est un. Ainsi, les modèles portant sur les mêmes espèces et conçus dans les mêmes circonstances doivent donner les mêmes conclusions sur les relations observées entre les poissons et leurs habitats pour qu'ils soient considérés comme stables dans le temps. Autrement dit, un habitat désigné comme étant excellent pour les poissons lors d'une visite donnée doit aussi être désigné comme excellent lors de la visite suivante. Alors que plusieurs caractéristiques environnementales des sites sont stables dans le temps, les descripteurs des communautés de poissons peuvent varier à l'intérieur d'une journée, entre les jours et/ou entre les années et influencer les conclusions des modèles. Dans le cadre de ce mémoire, les variations temporelles des descripteurs des communautés de poissons de quatre lacs des Laurentides ont donc été étudiées, ainsi que des moyens de diminuer ces variations temporelles.

Il a d'abord été montré que l'amplitude des variations entre les jours et entre les années était grande. En effet, la densité de poissons, tous groupes et tous lacs confondus variaient jusqu'à 209 fois entre les jours et 950 fois entre les années. Plusieurs de ces différences étaient statistiquement significatives, selon les résultats des nombreuses analyses de variance à deux critères de classification qui ont été faites. Par la suite, les mêmes analyses ont été refaites, mais en transformant les valeurs de densités de poissons aux sites en rangs, ou en groupant les sites en types d'habitats.

L'analyse des variations interjournalières ou interannuelles avec les rangs n'a pas été concluante, pour tous les groupes de poissons et tous les lacs. Dans tous les cas, les résultats étaient similaires à ceux obtenus lorsque les densités étaient utilisées directement. Cela suggère qu'un site ayant la plus forte densité de poissons à un jour donné d'une année donnée n'aura pas forcément la densité la plus élevée le jour suivant, de la même année ou non. Les poissons se déplacent donc entre les sites dans les différents lacs, sans montrer de fidélité à des sites particuliers et ce, autant entre les jours qu'entre les années.

Le groupement des sites en types d'habitats a par contre donné des résultats plus intéressants. En effet, plusieurs différences statistiquement significatives entre les jours et entre les années ont été éliminées lorsque les sites étaient groupés en types d'habitat. Les variations de densités et de rangs entre les jours et entre les années sont donc moindres lorsqu'on considère les types d'habitats plutôt que les sites dans les analyses. Ce phénomène suggère que les poissons se déplacent entre les sites de mêmes types d'habitat, démontrant une fidélité diffuse aux habitats plutôt qu'aux sites. D'une visite à l'autre, les poissons ne sont donc pas nécessairement aux mêmes sites, mais fréquentent de façon constante, à l'intérieur de l'échelle de temps considérée, les mêmes types d'habitat.

Ce mémoire souligne l'importance de considérer la variation temporelle des descripteurs des communautés de poissons lorsqu'on souhaite modéliser les relations entre les poissons et leurs habitats. Pour éviter l'influence indue des variations temporelles de densités sur les conclusions tirées des modèles, il semble important non seulement de faire plusieurs visites des mêmes sites, mais aussi de grouper les sites en types d'habitats. Cela peut permettre de dépeindre de façon adéquate l'importance moyenne des différents types d'habitats pour les communautés de poissons étudiées. La variation temporelle des descripteurs des communautés étant minimisée, cela devrait aussi permettre d'obtenir des modèles de qualité des habitats aux conclusions valides et intéressantes pour la préservation et la conservation des communautés de poissons étudiées.

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